LATE CAMPANIAN (CRETACEOUS)
HETEROMORPH AMMONITES FROM
THE WESTERN INTERIOR OF THE
UNITED STATES

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ABSTRACT

Heteromorph ammonites of the families Nostoceratidae Hyatt, 1894, and Diplomoceratidae Spath, 1926, are common to abundant in sediments deposited in the western and central parts of the U.S. Western Interior Seaway during the early late Campanian. The indices of the successive zones of *Didymoceras nebrascense* (Meek and Hayden, 1856a) (oldest), *Didymoceras stevensoni* (Whitfield, 1877), *Exiteloceras jenneyi camacki*, n. subsp., *Exiteloceras jenneyi jenneyi* (Whitfield, 1877), and *Didymoceras cheyennense* (Meek and Hayden, 1856a) are revised, as are *Nostoceras monotuberculatum* Kennedy and Cobban, 1993a (*D. nebrascense* and *D. stevensoni* zones), *Oxybeloceras crassum* (Whitfield, 1877) (*D. stevensoni* and *E. jenneyi* zones), and *Spiroxybeloceras meekanum* (Whitfield, 1877) (*D. cheyennense* zone). *Solenoceras elegans*, n. sp. (*D. stevensoni* and *E. jenneyi* zones), *Solenoceras bearpawense*, n. sp. (*D. nebrascense* zone), and *Solenoceras larimerense*, n. sp. (*E. jenneyi* zone) are also described.

INTRODUCTION

The ammonites described here are among the most striking and remarkable natural objects known from the Cretaceous rocks of the U.S. Western Interior, are important stratigraphic indicators, and are represented in museums throughout the world. They attracted the attention of the earliest geological surveying expeditions to the region. Thus, Meek and Hayden (1856a), Whitfield (1877), and Hyatt (1894) described new species of irregularly coiled, heteromorph ammonites from the Upper Cretaceous rocks of South Dakota and Wyoming under the names of *Ancyloceras? nebrascensis*, *Ancyloceras? cheyennensis*, *Ancyloceras? jenneyi*, *Ancyloceras (Hamites) uncus*, *Helicoceras angulatum*, *Helicoceras stevensoni*, *Emperoceras beecheri*, *Heteroceras simplicostatum*, *Ptychoceras crassum*, and *Ptychoceras meekanum*. Several of these species were based on single small fragments, which has led to considerable confusion as to the scope of the various species present. Other names are synonyms. Heteromorph ammonites are loosely coiled or even straight, and tend to be fragmented by wave and current action as well as by predation before fossilization. They are difficult to extract from the rock matrix, and most specimens are quite incomplete. Since the pioneer publications of Meek and Hayden (1856a, 1856b, 1858), Meek (1864, 1876), Whitfield (1877, 1880, 1901, 1902), and Hyatt (1894, 1900), collections made by members of the U.S. Geological Survey and by private collectors have revealed much new information about the growth stages and taxonomy of the species, as well as their stratigraphic and geographic distribution. The species described by the above authors are now known to be confined to the following four adjoining ammonite zones of Scott and Cobban (1965), from oldest to youngest: *Didymoceras nebrascense*, *Didymoceras stevensoni*, *Exiteloceras jenneyi*, and *Didymoceras cheyennense* (fig. 1), and are revised below, together with a number of new species of *Solenoceras* Conrad, 1860, *Nostoceras monotuberculatum* Kennedy and Cobban, 1993a, *Oxybeloceras crassum* (Whitfield, 1877), and *Spiroxybeloceras meekanum* (Whitfield, 1877).

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for us with other collectors. Steve Jorgensen, Omaha, Nebraska, allowed us to use photographs of some of his excellent specimens from the Pierre Shale of South Dakota. Harold Mendryk, New York, New York, donated many splendid heteromorphs that he collected in Wyoming and Colorado. Kennedy acknowledges the financial support of the Natural Environment Research Council (United Kingdom) and the technical assistance of the staff of the Geological Collections at Oxford University Museum of Natural History and the Department of Earth Sciences of Oxford University. Landman thanks Barbara Worcester, Portia Rollings, and Stephanie Crooms (all AMNH) for assistance in manuscript preparation.

**USGS MESOZOIC LOCALITIES MENTIONED IN THE TEXT**

Localities of heteromorph ammonites described or mentioned in the text are shown in figure 2. Locality numbers, names of collectors, years of collections, locality descriptions, and stratigraphic assignments of U.S. Geological Survey (USGS) Mesozoic localities are given in appendix 1. For details of some of the stratigraphic units and the stratigraphic positions of USGS collections in the zones of *Didymoceras nebrascense*, *Didymoceras stevensoni*, *Didymoceras cheyennense*, and *Exiteloceras jenneyi*, the reader is referred to the stratigraphic columns shown by Scott (1964, 1969), Scott and Cobban (1965, 1975, 1986a, 1986b), Gill and Cobban (1966), and Gill et al. (1970).

**CONVENTIONS**

Rib index refers to the number of ribs in a distance equal to the whorl height. The following prefixes are used to indicate the repositories of the specimens described or mentioned in the text: USNM (National Museum of Natural History, Washington, DC), BHMNH (Black Hills Museum of Natural History, Hill City, SD), and YPM (Peabody Museum of Natural History, Yale University, New Haven, CT). Specimens are illustrated at natural size unless otherwise indicated. Arrows on the photographs mark the position of the last suture where visible. Suture terminology follows that of Kullmann and Wiedmann (1970) where E is the external lobe, L is the first lateral lobe, and U is the umbilical lobe.

**DIMORPHISM**

The ammonites described below are in our view dimorphic, with larger macroconchs and smaller microconchs, the former interpreted as females, the latter as males. In some heteromorphs, such as the Scaphitaceae (see Cobban, 1969; Landman and Waage, 1993; Davis et al., 1996) dimorphs have different coiling and ornament, and there is an overlap in adult size between dimorphs. In other heteromorphs, including those described below, differences between dimorphs (other than size) are not developed, and although large and small adults occur and are interpreted as macro- and microconchs, there is a continuum in adult size, and not all individuals can be assigned to macro- and microconch. In the ensuing descriptions we have recognized dimorphism on the basis of subsets of large and small adult individuals in collections, but acknowledge that not all individuals can be so assigned. See Davis et al. (1996) for a full discussion of dimorphism in Cretaceous heteromorphs.
Fig. 2. Index map of part of the Western Interior of the United States showing localities of heteromorph ammonites described or mentioned in the text. Numbers refer to USGS Mesozoic localities listed in appendix 1.
SYSTEMATIC PALEONTOLOGY

SUBORDER ANCYLOCERATINA WIEDMANN, 1966
SUPERFAMILY TURRILITACEAE GILL, 1871
(= Diplomocerataceae Brunnschweiler, 1966: 14)

FAMILY NOSTOCERATIDAE HYATT, 1894
(= Jouaniceratidae Wright, 1952: 218; Bostryhoceratinae Spath, 1953: 16; Emperoceratinae Spath, 1953: 17; Hyphantoceratinae Spath, 1953: 16; Proavitoceratinae Spath, 1953: 17, errore pro Pravitoceratinae)

DISCUSSION: Hyatt (1894: 568) proposed this family for “a more or less artificial group . . . showing the common characteristics of several groups of phylogenic species . . . with unsymmetrical spirals in the ephic stages, more or less prominent costae and two rows of tubercles . . . the gerontic stages often have a retroversal living chamber and are tuberculated.” Hyatt assigned the new genera Nostoceras, Didymoceras, Emperoceras, and Exiteloceras to this family.

Since Hyatt’s pioneer work, the family Nostoceratidae has been enlarged to include many more genera, which may or may not have tubercles. Heteromorph genera, excluding baculites and scaphites, from rocks of Campanian and Maastrichtian age from the Western Interior, Gulf Coast, and Atlantic Seaboard, that can be assigned to this family include Nostoceras Hyatt, 1894, Anaklino- ceras Stephenson, 1941, Bostryhoceras Hy- att, 1900, Eubostryhoceras Matsumoto, 1967, Didymoceras Hyatt, 1894, Cirrocera Conrad, 1868, Axonoceras Stephenson, 1941, and Exiteloceras Hyatt, 1894.

Genus Didymoceras Hyatt, 1894
(= Emperoceras Hyatt, 1894: 575; Didymoceratoides Kennedy and Cobban, 1993a: 90)


DIAGNOSIS: Juvenile stage of either loose helical coils or loose straight limbs connected by elbows followed by a middle growth stage of helical whorls that may or may not be in contact; body chamber in a retroversal whorl.

DISCUSSION: Hyatt (1894: 573) proposed this genus for “. . . a series of forms having loose helicoidal spirals, two rows of more or less irregular ventral tubercles and irregularly bifurcated costae, which also have, or appear to have, a gerontic stage with a retroversal volution, as in Nostoceras. These are all larger shells and are separable by the helicoceran mode of growth in the ephic stage.” He assigned to his new genus the species Ancyloceras? nebrascense Meek and Hayden (1856a: 71), Turrilites (Helicoceras) cochleatus Meek and Hayden (1858: 55), and Helicoceras tortum Meek and Hayden (1858: 54). Hyatt also noted that Heteroceras newtoni Whitfield (1877: 40) and Ancyloceras tricostatus Whitfield (1877: 43) probably belonged to Didymoceras.

Hyatt (1894: 575) also proposed the new genus Emperoceras with Emperoceras beecheri as the type species, from the Pierre Shale of the same general locality as his specimen of Didymoceras nebrascense. The types of E. beecheri consist of two magnificent specimens that have early hamitid whorls in a plane followed by a spire of loose whorls not in contact with one another. Whitfield (1902: 68, pls. 23–27), apparently unaware of Hyatt’s work, described and figured several excellent specimens of E. beecheri under the name of Heteroceras simplicostatum Whitfield (1880), all from the same general area as Hyatt’s E. beecheri and D. nebrascense. As described below, all are synonyms of Didymoceras nebrascense; Emperoceras is thus a junior synonym of Didymoceras.

Kennedy and Cobban (1993a: 90) diagnosed their new genus Didymoceratoides (type species Didymoceras binodosum Kennedy and Cobban, 1993a: 92, figs. 8.1, 8.2, 8.5, 8.6, 8.13–8.15, 8.22–8.24, 8.28, 8.29, 8.32, 8.33, 8.35–8.39, 9.1–9.5, 12.1) as follows: “Early low open helix followed by loose elliptical criocone, ornamented by sharp rursiradiate ribs that weaken on dor- sum; all ribs bear ventral spines during early and middle growth; nontuberculate ribs in-
tercalate on adult body chamber; constrictions and flared ribs may be present; sutures deeply and intricately incised with bifid lobes and saddles.” They regarded Didymoceratoideas as a paedomorphic offshoot of Didymoceras. Subsequent work has shown that the symmetrical, planispiral body chambers present among the type series are body chambers of juvenile, rather than adult individuals. Adult D. binodosum have helical whorls and a recurved body chamber, as in typical Didymoceras, of which Didymoceratoideas is thus a synonym. Larson et al. (1997: 53, unnumbered fig.) have illustrated a reconstruction of the species.

The following Western Interior and Gulf Coast nominal species, with their original references and spellings, are here referred to Didymoceras; many are synonyms, as described below. The list is in alphabetical order by genus and then by species.

Ancyloceras cheyennensis Meek and Hayden, 1856a: 71.
Ancyloceras? nebrascense Meek and Hayden, 1856a: 71.
Ancyloceras? nicolletii Hall and Meek, 1856: 397, pl. 4, fig. 4.
Ancyloceras tricostatus Whitfield, 1877: 43, pl. 15, figs. 7, 8.
Ancyloceras (Hamites) uncus Meek and Hayden, 1858: 56.
Emperoceras beecheri Hyatt, 1894: 575, pl. 14, figs. 15–17.
Helicoceras angulatum Meek and Hayden, 1860a: 176.
Helicoceras mortoni var. tenuicostatum Meek, 1876: 487, pl. 22, fig. 3a–c.
Helicoceras navarroensis Shumard, 1861: 190.
Helicoceras stevensoni Whitfield, 1877: 39.
Helicoceras tenuicostatus Meek and Hayden, 1858: 56.
Helicoceras tortus Meek and Hayden, 1858: 54.
Helicoceras vespertinus Conrad, 1874: 455.
Heteroceras newtoni Whitfield, 1877: 40.
Nostoceras platycostatum Kennedy and Cobban, 1993b: 131, pl. 2, figs. 16, 17; pl. 4, figs. 1–13, 33, 34; text-fig. 7a.
Turrilites (Helicoceras) cochleatus Meek and Hayden, 1858: 55.
Turrilites? umblicatus Meek and Hayden, 1858: 56.

**OCCURRENCE:** Didymoceras is a common heteromorph in the zones of Baculites scotti, Didymoceras nebrascense, Didymoceras stevensoni, and Didymoceras cheyennense in the Bearpaw and Pierre shales in Montana; in the same zones as well as those of Baculites gregoryensis and B. scotti in the Pierre Shale in Wyoming and South Dakota; in the D. nebrascense and D. stevensoni zones in the Mesaverde Formation in Wyoming; in the Baculites reduncus and D. stevensoni zones in the Rock River Formation in Wyoming; in the D. nebrascense zone in the Pierre Shale in Kansas; in the B. gregoryensis, B. scotti, D. nebrascense, D. stevensoni, D. cheyennense, and Baculites reesidei zones in the Pierre Shale in Colorado; in the B. gregoryensis, B. scotti, and D. stevensoni zones in the Mancos Shale in Colorado; in the D. cheyennense zone in the Williams Fork Formation in Colorado; in the B. scotti zone in the Sego Sandstone in Utah; in the B. gregoryensis, D. nebrascense, and D. stevensoni zones in the Pierre Shale in New Mexico; and in the B. scotti, D. nebrascense, and D. cheyennense zones in the Lewis Shale in New Mexico. Didymoceras is also found in the Bergstrom Formation in Texas, Ozan Formation and Annona Chalk in Arkansas, Mount Laurel Sand in Delaware, and Wenonah Formation in New Jersey. Outside the United States, Didymoceras is known from Canada, Mexico, France (Kennedy and Bilotte, 1995), Spain (Martinez, 1982), Poland (Blaszkiewicz, 1980), Israel (Lewy, 1969), Egypt (Luger and Gröschke, 1989), Madagascar (Colignon, 1971), Angola (Howarth, 1965), and Nigeria (Zaborski, 1985).

**Didymoceras nebrascense** (Meek and Hayden, 1856a)

Figures 3, 4, 6, 7, 8C, D, 9–13, 62

Ancyloceras? Nebrascensis Meek and Hayden, 1856a: 71.

Turrilites Nebrascensis Meek and Hayden. Meek and Hayden, 1856b: 280.


Helicoceras Nebrascense Meek and Hayden. Meek and Hayden, 1860a: 185.

Helicoceras Nebrascense Meek and Hayden. Meek and Hayden, 1860b: 421.

Heteroceras? Nebrascense Meek and Hayden.
Fig. 3. Restoration of *Didymoceras nebrascense* (Meek and Hayden, 1856a). Stipple board drawing by John R. Stacy. Figure is reduced $\times 0.90$. 
Fig. 4. Part of the external suture of *Didymoceras nebrascense* (Meek and Hayden, 1856a). E is the external lobe and L is the lateral lobe. The heavy, straight line marks the middle of the venter. USNM 482435, USGS Mesozoic locality 21574 (fig. 2, loc. 2).

Meek, 1876: 480, pl. 22, fig. 1a–c (chevannense in explanation of plate).  
*non Heteroceras? nebrascense* Meek and Hayden.  
Whitfield, 1880: 451, pl. 14, fig. 9; pl. 15, fig. 6 (= *Helicoceras Stevensoni* Whitfield, 1877).  
*Heteroceras nebrascense* Meek and Hayden.  
Stanton, 1888: 186.  
*Heteroceras? nebrascense* (Meek and Hayden).  
Boyle, 1893: 148.  
*Emperoceras Beecheri* Hyatt, 1894: 575, pl. 14, figs. 15–17 (subjective synonym).  
*Didymoceras nebrascense* sp. Spath, 1921: 253.  
*Hamitoceras simplicostatum* Whitfield. Abel, 1924: text fig. 295c.  
*Turrilites (Heteroceras) nebrascense* Meek and Hayden. Diener, 1925: 91.  
*Cirroceras nebraskense* (sic) (Hyatt). Wright, 1957: L224, fig. 251.3.  
*Emperoceras simplicicostatum* (sic) (Whitfield). Wright, 1957: L224, fig. 251.5.  
*Didymoceras nebrascense* (Meek and Hayden). Scott, 1969: pl. 2 (unnamed fig.).  
*Didymoceras nebrascense* (Meek and Hayden). Gill and Cobban, 1973: 7, text fig. 5a.  
*Didymoceras nebrascense* (Meek and Hayden). Scott and Cobban, 1975: unnumbered fig.  
*Didymoceras nebrascense* (Meek and Hayden). Hirsch, 1975: text fig. 7a.  
*Cirroceras (Didymoceras) sp.* Case, 1982: fig. 12.36.  
*Didymoceras nebrascense* (Meek and Hayden). Scott and Cobban, 1986a: unnumbered fig.  
*Didymoceras nebrascense* (Meek and Hayden). Scott and Cobban, 1986b: unnumbered fig.  
*Didymoceras navarroense* (Shumard, 1861). Emerson et al., 1994: 313, part of unnumbered fig.  
*Didymoceras nebrascense* (Meek and Hayden). Kennedy and Bilotte, 1995: fig. 3A.  
*Nostoceras (Didymoceras) nebrascense* (Meek and Hayden). Wright, 1996: 247, fig. 191, 5.  
*Didymoceras nebrascense* (Meek and Hayden, 1856). Larson et al., 1997: 54, 3 unnumbered figs.  
*Didymoceras nebrascense* (Meek and Hayden). Sealey and Lucas, 1997: 235, fig. 4A–E.  

**Types:** The holotype, by monotypy, is USNM 469, from “Iquor creek, north fork, Cheyenne” (Meek and Hayden, 1856a: 71). The north fork of the Cheyenne River is now called the Belle Fourche River. Figured specimens are USNM 450333 and 482417–482435.  

**Material:** About 1000 fragments from
Fig. 5. Index map of part of the Western Interior of the United States showing localities of *Didymoceras nebrascense* (Meek and Hayden, 1856a). An x may indicate one or several nearby localities. Numbers refer to USGS Mesozoic localities listed in the text. Dashed line marks the approximate position of the western shoreline of the Western Interior Seaway during *D. nebrascense* zone time.
Fig. 6. *Didymoceras nebrascense* (Meek and Hayden, 1856a). A. USNM 482427, USGS Mesozoic locality D1421 (fig. 2, loc. 12). B. USNM 482428, USGS Mesozoic locality D1422 (fig. 2, loc. 13). Figures are ×1.
Fig. 7. Didymoceras nebrascense (Meek and Hayden, 1856a). USNM 482429, USGS locality D1422 (fig. 2, loc. 13). Figures are ×1.
Fig. 8. A, B. Didymoceras stevensoni (Whitfield, 1877). BHMNH 4039, collected by Howard Ehrle, Pierre Shale of Carter County, Mont. C, D. Didymoceras nebrascense (Meek and Hayden, 1856a). C. USNM 482430, USGS Mesozoic locality D85 (fig. 2, loc. 23). D. YPM 6131B, plaster cast of one of two specimens described by Hyatt (1894) as the new genus and species Emperoceras beecheri, Pierre Shale near Buffalo Gap, S. Dak. Figures are ×1.
Fig. 9. A, B. Didymoceras nebrascense (Meek and Hayden, 1856a). YPM 6131A, plaster cast of Hyatt's (1894) second specimen described as Empyroceras beecheri, Pierre Shale near Buffalo Gap, S. Dak. Figures are X1.
Fig. 10. *Didymoceras nebrascense* (Meek and Hayden, 1856a). USNM 482431, USGS Mesozoic locality D85 (fig. 2, loc. 23). Figure is \( \times 1 \).
100 localities. Most specimens are undeformed; nearly all are from limestone concretions. The largest collections consist of about 300 specimens (fragments) from USGS Mesozoic locality D2629 (fig. 2, loc. 3) and about 120 fragments from USGS Mesozoic locality D1421 (fig. 2, loc. 12).

**Diagnosis:** Earliest whorls are straight limbs connected by elbows and followed by a gently curved limb all in a loose planispiral. Middle growth stage is a loose helix of several whorls that are usually not in contact. Last part of body chamber bent in a U-shape with the aperture facing upward. Ornament consists of dense ribs and two rows of tubercles (fig. 3).

**Description:** The holotype, about a quarter of a poorly preserved septate, sinistral helical whorl, is about 50 mm long and has a circular cross section 23.5 mm in diameter at the smaller end. Twenty-one rounded ribs, narrower than the interspaces, cross the venter. The specimen is limonitic and contains much brown barite.

An ammonitella is not preserved in the collections. The smallest specimen observed (USNM 482417, not illustrated) from USGS Mesozoic locality 23381 (fig. 2, loc. 1) is a straight limb 28.3 mm long with end diameters of 1.0 mm and 2.7 mm. A furrow on the following elliptical whorl reveals that the smaller part of the straight limb extended at least 7 mm beyond the preserved part. Ornament consists of single, prorsiradiate ribs that bear small, nodate tubercles at the edge of the venter; the rib index is 4. Other small, straight limbs (USNM 482418, not illustrated) from USGS Mesozoic locality 23381 reveal small, sharp spines rising from the tubercles and constrictions at about every sixth
Fig. 12. A, B. Didymoceras nebrascense (Meek and Hayden, 1856a). USNM 482433, USGS Mesozoic locality D1422 (fig. 2, loc. 13). Figures are ×1.
Fig. 13. A, B. Didymoceras nebrascense (Meek and Hayden, 1856a). USNM 482434, USGS Mesozoic locality D1422 (fig. 2, loc. 13). Figures are ×1.
rib. Constrictions bordered by high adapical ribs and spaced at every fifth or sixth rib are present on some of the small, straight limbs (USNM 482419, 482420, not illustrated).

The shell curves into a narrow elbow at the larger end of the small, straight limb and then continues on as a second but larger straight limb that may parallel the smaller one, or form an acute angle of 10 to 30°. Whorl height of the larger limb increases more rapidly than width, producing an elliptical cross section. A constriction may be present on the elbow. Ribbing becomes rectiradiate on the elbow and then changes to rursiradiate on the larger limb. Ribs tend to be of irregular height on the larger limb. Some specimens (for example, USNM 482421, not illustrated, from USGS Mesozoic locality D2629) have tuberculate ribs that alternate in height with smaller nontuberculate ribs. Other specimens (for example, USNM 482422, not illustrated), may have every fourth or fifth rib flared on the early part of the limb.

The larger straight limb merges into a somewhat broadly curved elbow that leads to a gently curved limb. The cross section of the elbow and the curved limb is usually an inflated ellipse that is a little higher than wide. Ribbing on the elbow and curved limb is slightly rursiradiate to rectiradiate, and every second, third, or fourth rib bears a small nodate or flat-topped tubercle that supports a small, sharp spine (fig. 1IC). The rib index is 8–10; ribs cross the venter transversely. The larger end of the curved limb leads to a broadly curved elbow that merges into the helical spire (figs. 8D, 9A). Occasional individuals have an abbreviated planispiral stage of only one straight limb and one gently curved limb that merges into the helical stage.

The middle or helical growth stage (which can begin at quite small sizes: figs. 11A, B) consists of about three loosely coiled whorls that are either not in contact or just barely touch (figs. 3, 9B). Whorl sections are circular. Ribs are usually wirelike, narrower than the interspaces, closely spaced, and mostly single. The rib index is 10–14. Ribs are rursiradiate on the lower and outer whorl faces, but curve forward on the upper face and cross the dorsum in a slight convexity. Every few ribs, a rib bears small, nodate, bullate, or flat-topped tubercles in two rows of about equal size (fig. 3). Tubercles are generally matched, but they may alternate for short distances (fig. 9B). Occasional specimens that have flat-topped tubercles may also have flat-topped ribs (USNM 482423–482426). These flat-topped ribs and tubercles are on an inner layer of shell material and form the bases of an outer layer of hollow rounded ribs and nodate to bullate tubercles (fig. 9B). Tubercles usually disappear on the last half of the final helical whorl, which also includes the first part of the body chamber (figs. 6A, 9B, 10). The body chamber is long; it includes half to nearly all of the last whorl of the helix as well as a retroversal whorl that forms a U and curves back toward the helix (fig. 3). The intercostal section is subcircular and slightly higher than wide. Oblique ribbing, characteristic of the helix, continues on the older, twisted part of the body chamber. Ribbing becomes rectiradiate on the younger third of the body chamber, where the U-shaped whorl becomes planispiral (figs. 7, 13). Here ribs are transverse on the venter, where the rib index is 6–11. Tubercles are rejuvenated at the beginning of the uncoiled part of the body chamber; at first small and bullate, they rapidly enlarge into spine-bearing tubercles that are mostly nodate with some bullate and a few clavate (figs. 10, 13). They may be opposite on part of the body chamber and alternate on the remainder (fig. 7). Tubercles weaken and disappear rapidly near the adult aperture, where the last 6 to 11 ribs may be nontuberculate. The aperture is normal and follows the form of the ribbing (figs. 10, 12A, 13A).

Coiling is both dextral and sinistral (figs. 6, 8C, 9B). The collection from USGS Mesozoic locality D1421 (fig. 2, loc. 12) has 118 fragments of helical whorls, 62 dextral, 56 sinistral. USGS Mesozoic locality D1422 (fig. 2, loc. 13) has 70 helical fragments, 32 dextral, 38 sinistral. USGS Mesozoic locality D2629 includes 103 helical fragments, 54 dextral, 49 sinistral. The largest collection, 591 specimens of one-third of a whorl or more, collected by Steve Jorgensen (Omaha, NB) and members of the Black Hills Museum of Natural History, from the Pierre Shale at localities 11–13 (fig. 2) has 304 sinistral
and 287 dextral specimens (N. Larson, written commun., 1994).

*Didymoceras nebrascense* is dimorphic. Adults in the USGS collections are as small as 180 mm in height and as large as 270 mm in height, but the number of adults at hand is too few to determine the size ranges of microconchs and macroconchs. A microconch in the BHMNH collections has a body chamber 100 mm high; this incomplete individual probably had an original height of 140 mm (N. Larson, written commun., 1994).

The suture has expanded lateral and umbilical lobes (fig. 4). The saddles between the external and lateral lobes and between the lateral and umbilical lobes are deeply bifid.

**Discussion:** *Didymoceras nebrascense* is easily identified by its densely ribbed, loosely coiled helix of 3½ whorls followed by a large U-shaped body chamber. The poor and incomplete preservation of the holotype (less than half a whorl) led some previous workers to introduce several names for fragments of other ontogenetic stages and more complete specimens of *Heteroceras simplicostatum*, several well-preserved heteromorph ammonites from the Pierre Shale near Buffalo Gap, South Dakota. Whitfield’s specimens are very much like those of Hyatt’s from the Buffalo Gap area. All are excellent examples of *Didymoceras nebrascense*.

Healed injuries are scarce in the USGS specimens, and only three or four were observed in all the specimens examined. The injuries consist of a dent in the shell or some sort of a shallow groove that interrupts the ribbing for a few centimeters. The large BHMNH collection of 591 specimens has “44 injured conchs with most injuries present on the body chamber. Most injuries are tubercle and rib displacements of which seven specimens have a single row of tubercles along the venter. Fifteen specimens have dents, and four of these show healed ruptures or bites” (N. Larson, written commun., 1994).

**Occurrence:** *Didymoceras nebrascense* has been found at many localities along the western part of the Late Cretaceous seaway from northeastern Montana southward into northern New Mexico (fig. 5). Lewy (1969: 116, pl. 1, figs. 2a, b) recorded *Didymoceras* cf. *D. nebrascense* from the Mishash Formation of Israel. The Mishash specimen has hamitid whorls like those of *D. nebrascense*, but the ribbing is denser than that of *D. nebrascense*.

*Didymoceras stevensoni* (Whitfield, 1877)

*Figures 8A, B, 14–17, 19D–I, 20–26*


_Heteroceras? nebrascense* (Meek and Hayden).

Whitfield, 1880: 451, pl. 14, fig. 9; pl. 15, fig. 6.


_Heteroceras nebrascense*. Gilbert, 1896: pl. 64.


_Heteroceras stevensoni* (Whitfield). Scott, 1907: pl. 15, fig. 17.


Fig. 14. Restoration of most of a *Didymoceras stevensoni* (Whitfield, 1877). Stipple board drawing by John R. Stacy. Figure is reduced ×0.90.
Fig. 15. A–C. Three views of the holotype of *Helicoceras stevensoni* Whitfield, 1877 (from Whitfield, 1880: pl. 14, figs. 5–7). Figures are ×1.
Fig. 16. A–C. Restorations of parts of the juvenile whorls of *Didymoceras stevensoni* (Whitfield, 1877). Stipple board drawing by John R. Stacy. Figures are ×1.
Fig. 17. Part of the external suture of *Didymoceras stevensoni* (Whitfield, 1877). E is the external lobe and L is the lateral lobe. The heavy, straight line marks the middle of the venter. USNM 482436, USGS Mesozoic locality D4446 (fig. 2, loc. 47).

*Helicoceras stevensoni* Whitfield. Grabau, 1921: fig. 1754d.
*Turrilites (Helicoceras) Stevensonii* (Whitfield). Diener, 1925: 89.
*Heteroceras sp.* Schuchert and Dunbar, 1933: pl. 33, fig. 9.
*Helicoceras stevensoni* Whitfield. Stovall and Brown, 1954: 375, fig. 5.
*Didymoceras stevensoni* (Whitfield). Cobban, 1970: D72, figs. 1a–f, m, 2.
*Didymoceras stevensoni* (Whitfield). Gill and Cobban, 1973: 7, fig. 5b.
*Didymoceras stevensoni* (Whitfield). Hirsch, 1975: figs. 6b, 7b.

*Nostoceras (Nostoceras)* sp. Luger and Gröschke, 1989: 401, pl. 49, figs. 5, 9, 10.
*Didymoceras sp.* Eldredge, 1991: pl. 112.
*Didymoceras stevensoni* (Whitfield). Kennedy and Bilotte, 1995: pl. 49, fig. 1; pl. 51, figs. 1, 2; text fig. 3B.
*Didymoceras stevensoni* (Whitfield). Kennedy et al., 1995: pl. 3, figs. 12, 13, 18, 19.
*Didymoceras stevensoni* (Whitfield, 1877). Kennedy and Cobban, 1997: 69, figs. 5.6–5.8, 5.13–5.15, 5.18, 5.19, 8.4–8.11.
*Didymoceras stevensoni* (Whitfield, 1877). Larson et al., 1997: 55, unnumbered fig.

**Types:** The holotype, USNM 12307, came from "limestone of the Fort Pierre group, on the west side of Beaver Creek, southwest Black Hills" (Whitfield, 1877: 40). The specimen came from a limestone concretion in rocks now assigned to the upper part of the Pierre Shale below the Monument Hill Bentonitic Member in the Beaver Creek drainage northwest, west, or southwest of present day Newcastle, Weston County, Wyoming (fig. 2).

**Material:** About 550 specimens, mostly less than half a whorl, from about 70 local-
Fig. 18. Index map of part of the Western Interior of the United States showing localities of *D. stevensoni* (Whitfield, 1877). An x may indicate one or several nearby localities. Numbers refer to USGS Mesozoic localities mentioned in the text. Dashed line marks the approximate position of the western shoreline of the Western Interior Seaway during *D. stevensoni* zone time.
TABLE 1
Dimensions and Rib Counts of Didymoceras stevensoni (Whitfield, 1877)*

<table>
<thead>
<tr>
<th>USNM</th>
<th>D</th>
<th>U</th>
<th>Wb</th>
<th>Wh</th>
<th>Wb:Wh</th>
<th>Ribs per whorl</th>
</tr>
</thead>
<tbody>
<tr>
<td>482456a</td>
<td>41.1</td>
<td>13.5 (0.33)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>22</td>
</tr>
<tr>
<td>482456b</td>
<td>42.2</td>
<td>10.8 (0.26)</td>
<td>19.1</td>
<td>17.3</td>
<td>1.10</td>
<td>21</td>
</tr>
<tr>
<td>482456c</td>
<td>47.0</td>
<td>—</td>
<td>21.0</td>
<td>17.5</td>
<td>1.20</td>
<td>23</td>
</tr>
<tr>
<td>482456d</td>
<td>48.2</td>
<td>11.5 (0.24)</td>
<td>23.8</td>
<td>21.0</td>
<td>1.13</td>
<td>24</td>
</tr>
<tr>
<td>482456e</td>
<td>49.4</td>
<td>13.5 (0.27)</td>
<td>22.4</td>
<td>19.3</td>
<td>1.16</td>
<td>25</td>
</tr>
<tr>
<td>482456f</td>
<td>61.3</td>
<td>18.7 (0.31)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>27</td>
</tr>
<tr>
<td>482456g</td>
<td>62.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>25</td>
</tr>
<tr>
<td>482456h</td>
<td>62.1</td>
<td>14.9 (0.24)</td>
<td>31.4</td>
<td>26.1</td>
<td>1.20</td>
<td>30</td>
</tr>
<tr>
<td>482456i</td>
<td>64.6</td>
<td>19.3 (0.30)</td>
<td>29.1</td>
<td>25.5</td>
<td>1.14</td>
<td>27</td>
</tr>
<tr>
<td>482456j</td>
<td>66.0</td>
<td>18.0 (0.27)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>22</td>
</tr>
<tr>
<td>482456k</td>
<td>66.3</td>
<td>20.5 (0.31)</td>
<td>29.0</td>
<td>25.2</td>
<td>1.15</td>
<td>22</td>
</tr>
<tr>
<td>482456l</td>
<td>68.0</td>
<td>19.3 (0.28)</td>
<td>29.9</td>
<td>27.1</td>
<td>1.19</td>
<td>22</td>
</tr>
<tr>
<td>482456m</td>
<td>69.0</td>
<td>20.3 (0.29)</td>
<td>29.6</td>
<td>26.8</td>
<td>1.10</td>
<td>22</td>
</tr>
<tr>
<td>482456n</td>
<td>70.2</td>
<td>14.8 (0.21)</td>
<td>31.6</td>
<td>29.6</td>
<td>1.07</td>
<td>27</td>
</tr>
<tr>
<td>482456o</td>
<td>71.6</td>
<td>16.2 (0.23)</td>
<td>32.0</td>
<td>28.2</td>
<td>1.13</td>
<td>30</td>
</tr>
<tr>
<td>482456p</td>
<td>73.0</td>
<td>18.3 (0.25)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>23</td>
</tr>
<tr>
<td>482456q</td>
<td>78.4</td>
<td>17.4 (0.22)</td>
<td>36.2</td>
<td>32.8</td>
<td>1.10</td>
<td>23</td>
</tr>
<tr>
<td>482456r</td>
<td>80.6</td>
<td>20.4 (0.25)</td>
<td>36.0</td>
<td>30.2</td>
<td>1.19</td>
<td>23</td>
</tr>
<tr>
<td>482456s</td>
<td>90.0</td>
<td>21.0 (0.23)</td>
<td>41.8</td>
<td>35.1</td>
<td>1.19</td>
<td>21</td>
</tr>
</tbody>
</table>

* All specimens are from the Pierre Shale at USGS Mesozoic locality D454 near Newcastle, Wyoming. Measurements in millimeters. Abbreviations: D, shell diameter; U, umbilical diameter; Wb, whorl breadth at larger end; Wh, whorl height at larger end; Wb:Wh, ratio of whorl breadth to whorl height. Figures in parentheses are dimensions expressed as a ratio of shell diameter; dashes (—) indicate no measurement.

ities chiefly in Montana, Wyoming, Colorado, and New Mexico. Most specimens are from limestone or ironstone concretions. The largest collections include over 100 fragments from USGS Mesozoic locality D1234 near Pueblo, Colorado (fig. 2, loc. 54), and about 70 fragments from USGS Mesozoic locality D454 near Newcastle, Wyoming (fig. 2, loc. 17).

Diagnosis: High-spired, with variable loosely coiled early whorls, later whorls in contact, final uncoiled stage in form of recurved hook-like body chamber with aperture facing upward. Ornament consists of strong, narrow, bituberculate ribs, often separated by nontuberculate ribs (fig. 14).

Description: The holotype (figs. 15, 20C) is an uncrushed, dextrally coiled spire of three stout whorls of which the lower two are in contact. The spire has a height of 82 mm, a breadth of 58 mm, and an apical angle of about 31°. The ratio of the umbilical diameter to the shell diameter at the larger end is 0.26. All but the last 15 mm of the spire is septate. All whorls have broadly rounded flanks and narrowly rounded shoulders. Whorl cross sections are wider than high. Ribs arise on the umbilical wall, where they are curved and prorsiradiate. They are narrow, strong, and rursiradiate on the whorl flank. Thirty-seven ribs are present on the last whorl, and 35 on the penultimate. On much of the specimen, every other rib is bituberculate with about equally sized, fairly small tubercles. One row of tubercles is at midflank, the other near the base of the whorl. Tubercles are bulate to nodate and of irregular height; most are sharp, a few flat-topped. Occasional tubercles of the lower row give rise to paired ribs. The complex suture of the holotype was illustrated by Whitfield (1880: pl. 14, fig. 8).

An adult specimen consisting of a complete body chamber and three whorls of the spire was well illustrated but briefly described by Whitfield (1901). According to Whitfield’s illustrations, the specimen has a length of about 162 mm. Whitfield observed that the body chamber included the last half of the final whorl of the spire and the uncoiled part of the shell that bent down away...
from the spire and then curved upward toward it. The aperture is normal and follows the course of the ribbing.

The large USGS collections of *Didymoceras stevensoni* reveal three growth stages: a highly variable juvenile stage of loose coils or loose limbs, a middle helicoid stage in which some whorls are in contact, and a late uncoiled stage in which the recurved hook-like body chamber ends with an aperture facing upward (fig. 14). Most of the specimens at hand represent the middle helicoid stage.

The juvenile stage is quite variable; all specimens are uncoiled to some degree (fig. 16). The smallest individual available begins as an open planispiral coil followed by elliptical coiling (fig. 19G). Terminal whorl heights are 1.3 and 3.5 mm. Ornament is of single, straight, prorsiradiate ribs; the rib index is 3. The early whorls of another specimen (fig. 21A) consist of two parallel limbs followed by an elliptical whorl that merges into the main spire (fig. 16). Some specimens have a length (figs. 19E, F, 20A, B, 23B–D), others a much shorter uncoiled stage (fig. 20E). Ribs on these early whorls are usually single and rectiradiate (figs. 19E, 20A). Each rib supports a small, spinose tubercle (fig. 19F) that borders the slightly flattened venter. Opposite tubercles are connected across the venter by low transverse ribs; the rib index is 3–5.

The middle helicoid stage consists of three or four whorls of which two or three are in contact (fig. 20C, E). An impressed area is present on the upper whorl face of the younger of the two whorls in contact. Whorls are stout and have subcircular cross sections. Nineteen well-preserved whorls from USGS Mesozoic locality D454 near Newcastle, Wyoming, have ratios of whorl breadth to whorl height of 1.07–1.20 and ratios of umbilical diameter to shell diameter of 0.21–0.33 (table 1). The dorsum is either smooth or has very weak transverse ribs or striae of irregular height. Rectiradiate to rursiradiate ribs strengthen rapidly on the lower whorl face, and are rursiradiate on the flank. They bear two rows of tubercles. The ribs curve forward and then weaken greatly or disappear at the juncture of the flank and upper whorl face. Ribs may be single and connect opposite tubercles before continuing onto the upper whorl face, or may split into two ribs at the lower tubercle, connect the lower and upper tubercles as looped ribs, and then proceed on across the upper whorl face as a single rib or as paired ribs. On an occasional specimen, a rib crosses the lower whorl face to a lower tubercle and then splits into two ribs without intercepting an upper tubercle. Nontuberculate ribs are fairly common and may alternate with tuberculate ribs, as in the holotype (fig. 15). Nontuberculate ribs may extend across the entire flank or may be present only on the lower or upper part of the flank. The density of ribs of the helicoid stage is 21–30 per half whorl (table 1). Tubercles are rather small, bullate (fig. 22A, B), nodate (fig. 23C, D), flat-topped (figs. 19D, 23A), and rarely clavate. All apparently supported small, sharp spines (fig. 23C, D).

As noted by Whitfield (1901), the adult body chamber includes the last half of the final helicoid whorl of the spire followed by a loose retroversal whorl (fig. 14). The gap between the body chamber hook and the base of the helicoid spire is small. The cross section of the hook becomes circular, and the ribbing rectiradiate. Ribs become more closely spaced near the aperture (figs. 21B, 26D). Tubercles at first increase in size on the hook and then decrease greatly near the aperture, which follows the trend of the ribs.

*Didymoceras stevensoni* is coiled dextrally and sinistrally. A large collection from the Pierre Shale at USGS Mesozoic locality

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Fig. 20. *Didymoceras stevensoni* (Whitfield, 1877). A. USNM 482441, USGS Mesozoic locality D454 (fig. 2, loc. 17). B. USNM 482442, USGS Mesozoic locality D1387 (fig. 2, loc. 27). C. USNM 12307, holotype of *Helicoceras stevensoni* Whitfield, 1877. Whitfield (1877: 40) gave the locality as: “limestone of the Fort Pierre Group, on the west side of Beaver Creek, southwest Black Hills.” D. USNM 482443, same locality as B. E. USNM 482444, USGS Mesozoic locality 23528 (fig. 2, loc. 7). Figures are ×1.
Fig. 21. *Didymoceras stevensoni* (Whitfield, 1877).  
A. USNM 482445, USGS Mesozoic locality D1498 (fig. 2, loc. 56).  
B. USNM 482446, USGS Mesozoic locality D5789 (fig. 2, loc. 50). Figures are x1.
Fig. 22. *Didymoceras stevensoni* (Whitfield, 1877). A. USNM 482447, USGS Mesozoic locality D625 (fig. 2, loc. 62). B. USNM 482448, USGS Mesozoic locality D454 (fig. 2, loc. 17). Figures are x1.
Fig. 23. *Didymoceras stevensoni* (Whitfield, 1877). A. USNM 482450, USGS Mesozoic locality D1387 (fig. 2, loc. 27). B–D. USNM 482449, USGS Mesozoic locality D358 (fig. 2, loc. 25). Figures are ×1.

D1234 near Pueblo, Colorado (fig. 2, loc. 54), contains 145 fragments of helicoid spires; 77 are sinistral, 68 dextral. Of this large collection, only two individuals are pathologic. Neal Larson (written commun., 1994) noted that a collection made by Howard Ehrle, Miles City, Montana, from the Pierre Shale of Carter County, Montana, consists of 119 specimens of half a whorl or more, of which 62 are sinistral, and 57 dextral. Only one specimen in this large collection has an injury; it consists of a large groove along the venter accompanied by displaced ribs and tubercles.

The species is dimorphic. Microconchs are about one-half as large as macroconchs.

The suture is highly digitate (fig. 17). Lobes are greatly expanded and have narrow
Fig. 24. Didymoceras stevensoni (Whitfield, 1877). USNM 482451. Figures are ×1.
Fig. 25. Didymoceras stevensoni (Whitfield, 1877). USNM 482452, USGS Mesozoic locality 1720 (fig. 2, loc. 28). Figures are x1.
Fig. 26. *Didymoceras stevensoni* (Whitfield, 1877). A, B. USNM 482453, USGS Mesozoic locality D1387 (fig. 2, loc. 27). C. USNM 482454, same locality as A, B. D. USNM 482455, USGS Mesozoic locality D154 (fig. 2, loc. 17). Figures are ×1.
bases. Parts of the suture were illustrated by Whitfield (1880: pl. 14, fig. 8) and by Cobban (1970: fig. 2).

**DISCUSSION:** *Didymoceras stevensoni* differs from *Didymoceras nebrascense* chiefly in having the larger helical whorls in contact, and in having coarser and fewer ribs, and a body chamber in which the adult aperture is closer to the helix. The early whorls of *D. stevensoni* are also more helical.

**OCCURRENCE:** *Didymoceras stevensoni* has been found at many localities in the Western Interior fairly close to the western shore of the Late Cretaceous Seaway (fig. 18). Phosphatic fragments, formerly thought to be from the Marshalltown Formation in Delaware (Cobban, 1970), are now believed to be from the base of the Mount Laurel Sand (Kennedy and Cobban, 1997). Kennedy and Bilotte (1995) recorded *D. stevensoni* from France. The *Nostoceras (Nostoceras)* sp. of Luger and Gröschke (1989) from the upper Campanian of Egypt is probably *D. stevensoni*.

*Didymoceras cheyennense* (Meek and Hayden, 1856a)
Figures 27–31, 33–38

*Ancyloceras? cheyenensis* (sic) Meek and Hayden, 1856a: 71.
*Turrilites Cheyennensis* Meek and Hayden. Meek and Hayden, 1856b: 280.
*Ancyloceras (Hamites) uncus* Meek and Hayden, 1858: 56 (subjective synonym).
*Ancyloceras (Hamites) uncus* Meek and Hayden. Hayden, 1859: 685.
*Helicoceras angulatum* Meek and Hayden, 1860a: 176 (subjective synonym).
Fig. 28. Side view and cross section of the holotype of *Ancyloceras (Hamites) uncus* Meek and Hayden, 1858 (from Meek, 1876: pl. 21, fig. 1a, b). Figure is ×1.

*Helicoceras Cheyennense* (Meek and Hayden). Meek and Hayden, 1860a: 185.

*Helicoceras angulatum* (Meek and Hayden). Meek and Hayden, 1860b: 421.


*Heteroceras? Cheyennense* (Meek and Hayden). Meek, 1876: 483, pl. 21, fig. 2a, b.

*Heteroceras? uncum* Meek and Hayden. Meek, 1876: 409, pl. 21, fig. 1a, b.


*Heteroceras angulatum* Meek and Hayden. Boyle, 1893: 146.


*Exiteloceras (Heteroceras) angulatum* (Meek and Hayden). Logan, 1898: 514, pl. 108, fig. 2.

*Turrilites (Heteroceras) angulatum* Meek and Hayden. Diener, 1925: 90.

*Turrilites (Heteroceras) cheyennense* Meek and Hayden. Diener, 1925: 90.

*Hamites uncus* Meek and Hayden. Diener, 1925: 70.

*Exiteloceras* (Heteroceras) angulatum Meek. Adkins, 1928: 212.

*Didymoceras cheyennense* (Meek and Hayden). Gill and Cobban, 1973: 10, fig. 5c.

*Didymoceras cheyennense* (Meek and Hayden). Scott and Cobban, 1975: unnumbered fig.

*Didymoceras cheyennense* (Meek and Hayden). Scott and Cobban, 1986a: unnumbered fig.

*Didymoceras cheyennense* (Meek and Hayden). Scott and Cobban, 1986b: unnumbered fig.
Fig. 29. End (A), dorsal (B), and ventral (C) views of the holotype of *Helicoceras angulatum* Meek and Hayden, 1860b (from Meek, 1876: pl. 21, fig. 3a-c). Figures are ×1.


*Exiteloceras angulatum* (Meek and Hayden, 1876). Emerson et al., 1994: 310, 311, unnumbered figs.

*Didymoceras cheyennense* (Meek and Hayden). Kennedy and Bilotte, 1995: fig. 3C.


*Didymoceras cf. D. cheyennense*. Ward and Orr, 1997: figs. 5.7–5.9, 6.6, 6.7.

*Didymoceras cheyennense* (Meek and Hayden). Larson et al., 1997: 56, 2 unnumbered figs.

**Types:** The holotype, by monotypy, is USNM 470, from “Mouth Cheyenne river. No. 4 of series.” (Meek and Hayden, 1856a: 72). The specimen probably came from rocks now assigned to the DeGrey Member of the Pierre Shale in north-central South Dakota.

**Material:** About 170 specimens, mostly half a whorl or less. Most are from limestone...
Fig. 30. Restoration of *Didymoceras cheyennense* (Meek and Hayden, 1856a). Stipple board drawing by John R. Stacy. Figure is reduced \( \times 0.83 \).
concretions and are usually uncrushed. The largest collections contain about 35 fragments from the Pierre Shale at USGS Mesozoic locality D1794 near Fort Collins, Colorado, and about 30 fragments from the Pierre Shale at USGS Mesozoic locality D8784 near Pueblo, Colorado (fig. 2, locs. 37, 56, respectively).

Diagnosis: Juvenile growth stage consists of loose hamitid limbs coiled in a plane; middle growth stage is a loose helix; last growth stage is a long retroversal whorl in which aperture faces helix.

Description: The holotype of Didymoceras cheyennense (fig. 27) is part of an adult body chamber about 70 mm long; the costal whorl height near the larger end is about 38.5 mm, the costal whorl breadth is about 38.8 mm (ratio of whorl breadth to whorl height is 1.01; measurements from a plaster cast). The fragment has a slight twist that indicates it is an early part of the body chamber. Ribs are narrow, oblique, prospiriradiate, and widely spaced. Each rib bears a small nodate or bullate tubercle on one side. Ribs on the other side bear slightly larger nodate tubercles. Opposite tubercles are connected across the venter by low transverse ribs. One pair of opposite tubercles is connected by looped ribs. There are four tubercles in a distance equal to the whorl height.

The holotype of Ancyloceras uncus Meek and Hayden, 1858 (fig. 28), first illustrated by Meek (1876: pl. 21, fig. 1a, b), is a somewhat crushed adult body chamber in the form of a hook. The whorl height at the larger end is 41 mm. Flank ribs are single, narrow, prospiriradiate, and widely spaced on the older part, rursiradiate and more closely spaced on the younger part. Each rib bears a small nodate or bullate tubercle that borders the venter. Tubercles are reduced in size toward the aperture. Opposite tubercles are connected across the venter by a transverse rib.

The holotype of Helicoceras angulatum Meek and Hayden, 1860a (fig. 29), first illustrated by Meek (1876: pl. 21, fig. 3a–c), resembles the holotype of Didymoceras cheyennense in size and form. It is a 72.5 mm long fragment of the older part of an adult body chamber with a costal whorl breadth of 41.0 mm and a costal whorl height of 36.0 mm (ratio of whorl breadth to whorl height is 1.14; measurements from a plaster cast). The specimen has a slight twist that indicates it is an early part of the body chamber. Ribs are narrow, sharp, oblique, prospiriradiate, and widely spaced. Each rib bears a small, somewhat bullate tubercle on one side. Ribs on the other side bear slightly larger nodate tubercles. Opposite tubercles are connected across the venter by low transverse ribs. One pair of opposite tubercles is connected by looped ribs. There are four tubercles in a distance equal to the whorl height.

The USGS collections of Didymoceras cheyennense reveal three growth stages (fig. 30) somewhat similar to those of Didymoceras stevensoni. A very loose helicoid stage that includes some straight limbs characterizes the juvenile whorls (figs. 33B–E, 34). Middle growth is characterized by a loose helix that includes whorls not in contact (fig. 34). The final stage is a retroversal hook (figs. 30, 34, 37).

The earliest whorls observed consist of straight divergent limbs connected by a narrowly bent elbow. USNM 482457 (not illustrated), has two straight limbs meeting at an angle of 48°. The cross section is subcircular. The smaller limb has a whorl height of 3.5 mm and ornament of single, prospiriradiate, tuberculate ribs; the rib index is 4. Single, rursiradiate, tuberculate ribs (rib index of 4) characterize the younger limb, which has a
Fig. 32. Index map of part of the Western Interior of the United States showing localities of *Didymoceras cheyennense* (Meek and Hayden, 1856a). An x may indicate one or several nearby localities. Numbers refer to USGS Mesozoic localities mentioned in the text. Dashed line marks the approximate position of the western shoreline of the Western Interior Seaway during *D. cheyennense* zone time.
Fig. 33. *Didymoceras cheyennense* (Meeke and Hayden, 1856a). A. USNM 482463, USGS Mesozoic locality D1794 (fig. 2, loc. 37). B, C. USNM 482464, USGS Mesozoic locality D2740 (fig. 2, loc. 39). D, E. USNM 482458, USGS Mesozoic locality D804 (fig. 2, loc. 45). All figures are ×1.
Fig. 34. Didymoceras cheyennense (Meek and Hayden, 1856a). BHMNH 2100, collected by Neal L. Larson, Pierre Shale near Red Shirt, Shannon County, S. Dak. Figures are reduced ×0.88.
Fig. 35. *Didymoceras cheyennense* (Meek and Hayden, 1856a). A. USNM 482465, USGS Mesozoic locality D1794 (fig. 2, loc. 37). B, C. USNM 482466, USGS Mesozoic locality D1689 (fig. 2, loc. 51). D. USNM 482460a, USGS Mesozoic locality D2740 (fig. 2, loc. 39). Figures are ×1.

Whorl height of 4.4 mm. USNM 482458, from the same locality, is a larger hook-shaped, twisted limb that has terminal whorl heights of 7.8 and 13.6 mm (fig. 33D, E). Ribs are rectiradiate on the straighter part and rursiradiate on the curved part of the specimen. About every other rib bears small, sharp, bullate tubercles. Most juveniles in other collections, however, have loose helicoid coils that begin at smaller diameters. USNM 482459 (unfigured), from USGS Mesozoic locality D68 (fig. 2, loc. 43), has an elliptically coiled whorl that passes into a regular helix at a helical diameter of 30.7
Fig. 36. Didymoceras cheyennense (Meek and Hayden, 1856a). A. USNM 482467, USGS Mesozoic locality D221 (fig. 2, loc. 14). B. USNM 482468, USGS Mesozoic locality D194 (fig. 2, loc. 37). Figures are ×1.
Fig. 37.  A, B. Didymoceras cheyennense (Meek and Hayden, 1856a). BHMNH 2139, collected by Neal Larson, Pierre Shale near Red Shirt, Shannon County, S. Dak. Figures are reduced ×0.83.
mm; the ratio of umbilical diameter to shell diameter is 0.62.

Loose, but evenly coiled, helicoid whorls characterize the middle growth stage (figs. 30, 33A, 35A, D). Four helices, from USGS Mesozoic locality D2740 (fig. 2, loc. 39), have diameters of 19.0–24.2 mm and ratios of umbilical diameter to shell diameter of 0.36–0.40 (USNM 482460a–d). Ratios of whorl breadth to whorl height are 1.08–1.18. The oblique ribs are rursiradiate on the outer whorl flank (venter) and lower whorl face and prorsiradiate on the upper whorl face and dorsum.

Ribs and tubercles are variable in middle growth. Tubercles of the lower row usually arise from single ribs, but tubercles of the upper row may give rise to paired ribs that cross the upper part of the flank and continue on across the upper whorl face (fig. 33A). An occasional rib extends from a lower tubercle and crosses the rest of the flank without giving rise to an upper tubercle, or a single rib may pass between two lower tubercles and
support an upper tubercle before continuing across the upper whorl face. Rarely, three ribs arise from a lower tubercle, and one may connect to an upper tubercle. More common are nontuberculate ribs separating some of the tuberculate ones (fig. 38C). Looped ribs that connect opposite tubercles may be present here and there. Tubercles are bullate, nodate, or flat-topped. Three or four tubercles are present in a distance equal to the whorl height; the rib index is 7–10 on the upper whorl face.

The third growth stage is marked by a final whorl that separates away from the spire and bends downward for a considerable distance before recurving to form a long hook with the aperture facing upward toward the spire (fig. 37). As a result, the body chamber begins at the end of the last whorl of the spire or beyond. The adult whorl is twisted somewhat as it separates from the spire; this condition results in oblique ribbing on about one-third of the uncoiled whorl (fig. 34). Beyond the initial twisted area, the body chamber becomes swollen, and ribbing becomes transverse and coarse. Ribs on the body chamber are single, prosiradiate on the older part, rectiradiate on the curve of the hook, and rursiradiate on the rest of the whorl (fig. 36B). Tubercles are mostly nodate and largest around the hook; they decline in size toward the aperture but generally persist to it. Opposite tubercles are usually matched across the slightly flattened venter and are connected by very low, broad ribs, but occasional tubercles may alternate on the hook. Four or five tubercles are present in a distance equal to the whorl height. The aperture follows the course of the ribbing, and is usually preceded by a few closely spaced ribs or by ribs of irregular height. The suture is complexly digitate and much like that of Didymoceras stevensoni (compare figs. 17 and 31).

The species is dimorphic. Microconchs (fig. 34) are about one-half as large as macroconchs (fig. 37).

Didymoceras cheyennense is coiled dextrally and sinistrally. Of 12 specimens from USGS Mesozoic locality D2740 (fig. 2, loc. 39), seven are dextral and five sinistral. Of 19 specimens from USGS Mesozoic locality DI794 (fig. 2, loc. 37), 7 are dextral, 12 sinistral. A large collection of 326 specimens a quarter whorl or more made by Steve Jorgensen and Neal Larson from the Pierre Shale southeast of Rapid City, South Dakota (fig. 32), includes 158 sinistral, and 168 dextral specimens (N. Larson, written commun., 1994). Thirty-seven have tubercle injuries that result in a single row of tubercles or in a displacement of the tubercles. Twenty-one specimens have constrictions, dents, or healed injuries due to bites.

Discussion: Ancyloceras (Hamites) uncus Meek and Hayden (1858) is based on a crushed hook of a small macroconch of Didymoceras cheyennense; Helicoceras angulatum Meek and Hayden (1860a) is based on the early part of a body chamber of a macroconch; both came from the Pierre Shale in the Cheyenne River valley east of the Black Hills in western South Dakota.

Didymoceras cheyennense typically consists of 2.5–3 narrow, loosely coiled whorls and a very long retroversal body chamber. The species differs from Didymoceras stevensoni in its longer retroversal whorl, fewer and looser helical whors, and finer ribbing. D. cheyennense is not as densely ribbed as Didymoceras nebrascense.

Occurrence: Didymoceras cheyennense has been found at many localities from central Montana southward into northern New Mexico. These localities are in the western part of the Late Cretaceous seaway (fig. 32). The species is also present in the basal part of the Mount Laurel Sand in Delaware. Ward and Orr (1997) recorded the species from Tercis (Landes) in southwest France.

Genus Nostoceras Hyatt, 1894

Type species: Nostoceras stantoni Hyatt, 1894: 570, by original designation (= Ancyloceras approximans Conrad, 1855).

Hyatt designated Nostoceras stantoni as the “genotype” without a description, but he did describe, without illustrations, three varieties: retrosum, prematurum, and aberrans. Stephenson (1941: 407, pl. 80) treated the variety retrosum as N. stantoni sensu stricto, the type species. Hyatt had two specimens of his variety retrosum, and these were redescribed and illustrated by Stephenson (1941: 408, pl. 80, figs. 2–5) as cotypes of N. stantoni (USNM 23278a, 23278b). One cotype (USNM 23278a) is a nearly complete helical
spire, and the other (USNM 23278b) is a similar spire plus a complete retroversal body chamber.

**Diagnosis:** Hyatt (1894: 569) proposed this genus for species that have “a close-coiled unsymmetrical shell during the ephebic stage and are true turrilitids. There are two rows of ventral tubercles, which become more or less deflected during development towards the lower side (whether this be the left or right side) of the whorls. There is a contact furrow which is maintained as long as the whorls are sufficiently close coiled and then disappears on the free gerontic volution. This volution is excentric and then recurved as in all retroversal living chambers ... the nepionic and perhaps earlier neanic substages ... is not a normal ammonoidal spiral, but an open, whorled, irregular shell of some kind ... the gerontic volution is apt to have tubercles even when they are absent in the ephebic stage.”

**Discussion:** Hyatt (1894: 573) also assigned to *Nostoceras*, *Turrilites helicinus* Shumard (1861: 191). Although Hyatt lacked the very earliest growth stages of *Nostoceras stantoni* and *Nostoceras helicinum*, he had indications of an open whorl or two in as much as the smallest whorl on some specimens lacked a contact furrow. Specimens of *N. stantoni* and *N. helicinum* in the collections at hand also lack the earliest whorl or two, but *Nostoceras alternatum* (Tuomey, 1854), from slightly younger rocks, clearly has a minute loosely coiled apex (Cobban, 1974: fig. 5).

Hyatt did not record constrictions in his descriptions of the varieties of *Nostoceras stantoni* and *Nostoceras helicinum*, but they are clearly visible in the specimens illustrated by Stephenson (1941: pl. 80). The constrictions are deep, parallel to the ribs, and number three to five per whorl. A high rib may border a constriction on one side or the other, or high ribs may bound both sides.

Species of *Nostoceras* show marked sized dimorphism. *Nostoceras* is thus a heteromorphic ammonite characterized by a dextral or sinistral helical spire of whorls mostly in tight contact and a partly to wholly uncoiled body chamber. Ornament consists of ribs, two rows of tubercles, and constrictions. The type species, *Nostoceras stantoni*, comes from close to the Campanian-Maastrictian boundary, and all other species that seem assignable to *Nostoceras* by the present authors are of Campanian or Maastrictian age. *An-cyloceras? approximans* Conrad (1855: 266, 1860: pl. 47, fig. 4), from the Saratoga Chalk of Arkansas, is a microconch of *N. stantoni* Hyatt, 1894, and *approximans* is thus the prior name for the species.

The following Western Interior, Gulf Coast, and Atlantic Seaboard species, with their original references and spellings, are considered *Nostoceras* by the present authors. The list is in alphabetical order by genus and then by species.

*Nostoceras? approximans* Conrad, 1855: 266.  
*Nostoceras colubriformis* Stephenson, 1941: 412, pl. 81, figs. 1–3.  
*Nostoceras dracos* Stephenson, 1941: 413, pl. 82, figs. 5–9.  
*Nostoceras helicinum crassum* Stephenson, 1941: 412, pl. 81, figs. 7, 8.  
*Nostoceras helicinum humile* Stephenson, 1941: 412, pl. 81, figs. 4–6.  
*Nostoceras hyatti* Stephenson, 1941: 410, pl. 81, figs. 9–12.  
*Nostoceras mordryki* Cobban, 1974: 13, pl. 10, figs. 1–17, text-fig. 11.  
*Nostoceras pulcher* Kennedy and Cobban, 1993a: 85, figs. 6.1–6.13, 12.2, 12.3.  
*Nostoceras stantoni* Hyatt, 1894: 570 (= *N. approximans*).  
*Nostoceras stantoni aberrans* Hyatt, 1894: 572 (= *N. approximans*).  
*Nostoceras stantoni prematurum* Hyatt, 1894: 572 (= *N. approximans*).  
*Turrilites alternatus* Tuomey, 1854: 168.  
*Turrilites helicinus* Shumard, 1861: 191.  
*Turrilites pauper* Whitfield, 1892: 268, pl. 45, figs. 1–5.  
*Turrilites saundersorum* Stephenson, 1941: 416, pl. 83, figs. 6–8.  
*Turrilites splendidus* Shumard, 1861: 191.

**Occurrence:** *Nostoceras* occurs in the Western Interior in the lower Maastrictian zone of *Baculites eliasi* in the Pierre Shale.
in Colorado, in the upper Campanian zones of *Baculites reesidei* and *Baculites jenseni* in Colorado, in the *B. reesidei* zone in the Lewis Shale in Wyoming, in the upper Campanian zone of *Didymoceras nebrascense* in the Pierre Shale in South Dakota, and in the upper Campanian zone of *Didymoceras stevensoni* in the Mancos Shale in Colorado. The genus is also found in the Neylandville Marl and Nacatoch Sand in Texas; in the Ozan Formation, Annona Chalk, and Saratoga Chalk in Arkansas; in the Ripley Formation in Tennessee, Mississippi, Alabama, and Georgia; in the Prairie Bluff Chalk in Mississippi; in the Mount Laurel Sand in Delaware; and in the Navesink Formation in New Jersey.

Outside the United States, *Nostoceras* occurs in Columbia (Kennedy, 1992), The Netherlands (Kennedy, 1987), Belgium (Kennedy, 1993), France (Kennedy, 1986), Spain (Martinez, 1982; Ward and Kennedy, 1993), Austria (Kennedy and Summersberger, 1984), Bulgaria (Tzankov, 1964), Poland (Blaszkiewicz, 1980), Russia (Mikhailov, 1951), Israel (Lewy, 1967, 1969), Libya (Lefeld and Uberna, 1991), Madagascar (Collignon, 1971), Angola (Howarth, 1965), Zululand (Spath, 1921), Australia (Henderson et al., 1992), and Japan (Matsumoto, 1977).

*Nostoceras monotuberculatum* Kennedy and Cobban, 1993a

Figure 19A–C


**Types:** The holotype is USNM 441493; paratypes are USNM 441494–441501, all from the basal phosphatic bed of the Annona Chalk at USGS Mesozoic locality D8826 near Yancy, Hempstead County, Arkansas.

**Material:** Three fragments, one less than a whorl, one a little more than a whorl, and one of two whorls.

**Diagnosis:** Helical whorls in tight contact, apical angle low. Ornament consists of constrictions, closely spaced ribs, and a row of small tubercles at midflank.

**Description:** The smallest specimen, BHMNH 4038 (plaster cast USNM 482469), consists of two dextral whors that were embedded in a body chamber of *Didymoceras nebrascense*. The specimen is 28 mm high with an apical angle of 18°. The whors are 19 and 23 mm in diameter. The lower and outer whor faces are broadly rounded; all of the upper whor face is occupied by a dorsal furrow. Ribs on the outer whor face are narrow, slightly flexuous, and rursiradiate. A few deep constrictions parallel ribs. The number of ribs per whor cannot be determined because of imperfect preservation.

USNM 482470 (fig. 19A, B), an internal mold, consists of 1.25 dextral whors with an apical angle of about 18° and a diameter of 24.7 mm. The lower and outer whor faces are broadly rounded; all of the upper whor face is occupied by a dorsal furrow. Ribs are wirelike and narrower than the interspaces; 44 ribs per whor are present on the middle of the outer whor face. Ribs are markedly rursiradiate and slightly flexuous on the outer whor face, curving forward a little at the junctures with the upper and lower whor faces. Most ribs bear a very small tubercle at midflank. Three deep constrictions, parallel to the ribbing and bordered by high adapical or adoral ribs, are present per whor. The specimen is probably entirely septate, but details of the suture are not visible.

The largest specimen, BHMNH 2093 (plaster cast USNM 482470, fig. 19C), consists of a nonseptate dextral whor with a scrap of the preceding whor. Most of the shell material is retained. The specimen has a diameter of 97 mm and a whorl height of 25 mm. The roundness of the whor faces is like that of the smaller specimens. Ribs are dense on the outer whor face, flexuous, rursiradiate, and about 30 per half whor at midflank. A single deep constriction bordered by a high adapical rib is present. About every other rib bears a small, sharp bullate tubercle at midflank.

**Discussion:** *Nostoceras pulcher* Kennedy and Cobban (1993a: 85, figs. 6.1–6.10, 7.61–6.13, 12.2, 12.3), the only other American *Nostoceras* that has a single row of tubercles, differs from *Nostoceras monotuberculatum* in having fewer and larger tubercles, a larger apical angle, and a wider umbilicus.

**Occurrence:** USNM 482470 came from a
phosphate-nodule bed at the top of a conspicuous sandstone unit in the Mancos Shale at USGS Mesozoic locality D7028 (fig. 2, loc. 46) near Aspen, Colorado (Freeman, 1972), identified by Cobban as Nostoceras cf. N. pauper. That sandstone unit is now considered the Cozzette Sandstone Member of the Iles Formation (Freeman, in Madden, 1989: 7). Diagnostic fossils were not found with the Nostoceras, but Didymoceras stevensoni was collected just above and just below the sandstone in the Aspen area. The other specimens, collected by N. L. Larson, are from the zone of Didymoceras nebrascense in the Pierre Shale of Fall River County, South Dakota. BHMNH 2093 is from the N½ sec. 13, T. 7 S., R. 7 E.; BHMNH 4038 is from the SW½ sec. 18, T. 7 S., R. 8 E.

The holotype of Nostoceras monotuberatum is from the base of the Annona Chalk near Yancy, Hempstead County, Arkansas. The specimen and the associated fossils are phosphatic. Inasmuch as N. monotuberatum occurs in the zones of Didymoceras nebrascense and Didymoceras stevensoni in the Western Interior, the phosphatized basal Annona bed may be a condensed section that represents both of these zones.

**Genus Exiteloceras** Hyatt, 1894

**Type Species:** Ancyloceras jenneyi Whitfield, 1877, p. 42, by the subsequent designation of Diener, 1925, p. 88.

**Diagnosis:** Planispiral, loosely coiled, earliest whorls hamitid with two or more open shafts connected by elbows. Adult whorls somewhat hamitid to criocone. All whorls have subelliptical cross sections. Ornament of narrow ribs bearing small, sharp spines (fig. 47). Size dimorphism present.

**Discussion:** Specimens of the type species are quite variable in their form, but most have hamitid early growth stages, becoming open criocone when adult. The genus is represented only by the type species in the area under consideration.

**Exiteloceras** has been referred to both Nostoceratidae and Diplomoceratidae by previous authors. We place it in the former with no great confidence, given the uncertainty surrounding its phylogenetic relationships.

**Occurrence:** Exiteloceras occurs in the Western Interior in the upper Campanian zone of Exiteloceras jenneyi. Specimens have been found in the Bearpaw Shale in Montana; the Pierre Shale in Montana, Wyoming, South Dakota, Colorado, and New Mexico; the Lewis Shale in Colorado and New Mexico; and in the Mancos Shale and Rifle shale unit of the Iles Formation in Colorado. The genus has also been found in the Navesink Formation in New Jersey, the Mount Laurel Sand in Delaware, the Ripley Formation in Mississippi, and in Colombia (Kennedy, 1992).

**Exiteloceras jenneyi jenneyi** (Whitfield, 1877)

Figures 40, 42, 43, 44A–C, 45–48

Ancyloceras Jenneyi Whitfield, 1877: 42.

Ancyloceras Jenneyi Whitfield. Whitfield, 1880: 452, pl. 15, fig. 5; pl. 16, figs. 7–9.


Exiteloceras jenneyi (Whitfield). Grabau and Shimer, 1910: 205, fig. 1474.


Exiteloceras jenneyi (Whitfield). Wright, 1957: L224, fig. 251, 7.


Exiteloceras jenneyi (Whitfield). Hirsch, 1975: fig. 8a–c.


Exiteloceras jenneyi (Whitfield). Bryant and Martin, 1988: fig. 23.

Fig. 39. Scatter diagram showing ratios of whorl breadth to whorl height of *Exiteloceras jenneyi jenneyi* (Whitfield, 1877), based on nine specimens from USGS Mesozoic locality D9651 (●), nine specimens from USGS Mesozoic locality D13451 (△), and the holotype (△) and of *E. jenneyi camacki*, n. subsp., based on 11 specimens from USGS Mesozoic localities D454, D851, D1232, D2619, D13448, and D13510 (○) and the holotype (+).

*Exiteloceras jenneyi* (Whitfield). Wright, 1996: 250, fig. 195, 1a–d.


*Exiteloceras jenneyi* Whitfield, 1877. Larson et al., 1997: 45, unnumbered figs.

**Types:** The holotype and paratype have USNM number 12295. They came from “limestone referred to the Fort Pierre Group of the Upper Missouri Cretaceous, on the East Fork of Beaver Creek, three miles west of Camp Jenney, Black Hills” (Whitfield, 1877: 43). Beaver Creek is a southeastward-flowing stream that joins the Cheyenne River south of Newcastle on the west flank of the Black Hills in eastern Wyoming. The specimens came from a limestone concretion(s) in rocks now assigned to the upper part of the Pierre Shale (lower and middle parts of the Monument Hill Bentonitic Member or from the upper part of the underlying shale; Robinson et al., 1964: 89–93).

**Material:** Abundant specimens come from over 100 localities mainly in Montana, South Dakota, Wyoming, and Colorado. Most specimens are from limestone concretions, and preservation is generally good. The largest collections consist of 61 specimens (USGS Mesozoic locality D304) and 48 specimens (USGS Mesozoic locality D2854), both from the Terry Sandstone Member of the Pierre Shale near Fort Collins, Colorado (fig. 2, locs. 35, 36).

**Diagnosis:** A moderate-sized planispiral species characterized by juvenile loose, elliptical coiling and by adult loose, circular coiling. Ornament of mostly single ribs, each of which bears a small spinose tubercle at the margin of the venter. Suture deeply and intricately subdivided.

**Description:** The holotype (fig. 42B, C) consists of parts of a phragmocone and much of the body chamber of a fairly small specimen (microconch?). Coiling is planispiral and broadly elliptical; the preserved part of the larger limb has a diameter of about 95 mm (measurements from a plaster cast). Whorl cross sections are oval with a broadly rounded dorsum. The flanks are very broadly rounded and converge to a fairly narrow venter that is narrowly rounded in intercostal

Fig. 40. Suture of *Exiteloceras jenneyi jenneyi* (Whitfield, 1877). E is the external lobe, L is the lateral lobe, U is the umbilical lobe, and I is the internal lobe. The heavy, straight line marks the middle of the venter. USNM 482478, USGS Mesozoic locality D1947 (fig. 2, loc. 19).
Fig. 41. Index map of part of the Western Interior of the United States showing localities of *Exiteloceras jenneyi* (Whitfield, 1877). An x may represent one or several nearby localities. Numbers refer to USGS Mesozoic localities mentioned in the text. Dashed line marks the approximate western shoreline of the Western Interior Seaway during *E. jenneyi* zone time.
Fig. 42. *Eusteleceras jenneyi jenneyi* (Whitfield, 1877). A, USNM 482482, USGS Mesozoic locality D304 (fig. 2, loc. 35). B, C, USNM 12295, holotype, from "limestone of the Fort Pierre Group, on the west side of Beaver Creek, southwest Black Hills" (Whitfield, 1877: 40).

Figures are x1.
Fig. 43. A–C. Exiteloceras jenneyi jenneyi (Whitfield, 1877). USNM 450341, from USGS Mesozoic locality D2854 (fig. 2, loc. 36). Figures are ×1.
Fig. 45. *Exiteloceras jenneyi jenneyi* (Whitfield, 1877). A. USNM 482484, USGS Mesozoic locality D304 (fig. 2, loc. 35). B. USNM 482485, same locality. Figures are ×1.
Fig. 46. *Exiteloceras jenneyi jenneyi* (Whitfield, 1877). A, B. USNM 482486, USGS Mesozoic locality 1338 (fig. 2, loc. 59). C–E. USNM 450342, USGS Mesozoic locality D79 (fig. 2, loc. 52). Figures are ×1.
Fig. 47.  *Exiteloceras jenneyi jenneyi* (Whitfield, 1877).  A. USNM 482487, USGS Mesozoic locality D304 (fig. 2, loc. 35).  B, C. Private collection of the late Karl F. Hirsch, Denver, Colo., Pierre Shale of the Pueblo area, Colo. Figures are ×1.
Fig. 48. *Euteloceras jenneyi jenneyi* (Whitfield, 1877). BHMNH 2140, collected by Howard Ehrle, Pierre Shale in Carter County, Mont. Figure is reduced ×0.92.
section and flattened in costal section. The maximum breadth of the whorl is a little below the middle of the flank. The ratios of whorl breadth to whorl height at two places on the outer whorl are 0.75 and 0.77 (fig. 39). Ornament consists of narrow ribs and a row of small tubercles on each side of the venter. Ribs are much narrower than the interspaces; they arise on the outer part of the dorsum and become highest on the lower half of the flank. Ribs are rursiradiate, most are slightly flexuous, and all support a small tubercle at the margin of the venter. An occasional weak secondary rib arises on the outer part of the flank and supports a ventral tubercle. All opposite tubercles are connected by a flattened rib that crosses the venter transversely. In places the flattened rib supports barely discernible looped ribs. Tubercles of the holotype are nodate to slightly bullate; many are flattened bases of septate spines. The rib index ranges from 5 to 6. The sutures of the holotype and paratype were illustrated by Whitfield (1880: pl. 15, fig. 5, pl. 16, fig. 9). Lateral and umbilical lobes are narrow-stemmed, expanded, and considerably denticulate. The saddles that separate ventral, lateral, and umbilical lobes are about equal in size and deeply bifid.

The bulk of the specimens of *Exiteloceras jenneyi* at hand are similar to the types, and have ratios of whorl breadth to whorl height between 0.7 and 0.8; the stouter form of the species that occurs low in the zone of *E. jennyi* is treated herein as the new chronologic subspecies *E. jenneyi camacki*. The earliest growth stage of *Exiteloceras jenneyi jenneyi* observed is a straight limb 19.2 mm long (USNM 482472, not illustrated). The whorl heights at the ends are 0.7 mm and 1.6 mm. Ornament is lacking except near the larger end, where barely discernible ventral tubercles arise. A later growth stage is shown in USNM 482473 (fig. 44A). This has a straight limb that bends into a broadly elliptical, open planispiral coil followed by a circular coil. Juvenile coiling varies considerably. Some specimens have at least three subparallel limbs connected by narrowly curved to broadly curved elbows (fig. 46D), whereas others have circular coiling at a small diameter (fig. 45A). Adult specimens have circular to somewhat elliptical coiling (fig. 43B). The largest specimen (USNM 482474, not illustrated) in the USGS collections is a fragment of a body chamber 74 mm in whorl height from USGS Mesozoic locality D439 (fig. 2, loc. 15).

Ornament of *Exiteloceras jenneyi jenneyi* consists of narrow ribs that are generally rursiradiate. A few ribs may be rectiradiate, and a very few may be prorsiradiate. In this respect, the drawing of *E. jenneyi* presented by Scott and Cobban (1965) and reproduced in many works is not typical of the species; the drawing shows dominantly rectiradiate and prorsiradiate ribbing. Ribs of *E. jenneyi jenneyi* are usually single and arise on the outer part of the dorsum. An occasional secondary rib may arise high on the flank and supports a small ventral tubercle. The holotype has several of these short secondary ribs on the outer whorl (fig. 42C). An unusual individual (USNM 482475, not illustrated, from USGS Mesozoic locality 79) (fig. 2, loc. 52), is a segment of an adult body chamber that has six consecutive primary ribs each separated from the rest by a short tuberculate secondary rib. Beginning at a whorl height as small as 13 mm, ribs may become somewhat flexuous (fig. 45A); they are especially flexuous and closely spaced near the aperture (fig. 46D). On many specimens, ventral ribs are represented by paired looped ribs that connect opposite tubercles (fig. 47B). Every rib on the flank supports a tubercle that borders the venter. Tubercles may be clavate, bullate, or nodate. Some are flat-topped, but all supported small, hollow spines (figs. 44A, C, 47A). In general, there are 5–7 tubercles in a distance equal to the whorl height; a few specimens have 3 or 4 and a few 8–10 in a distance equal to the whorl height.

Adult specimens show a reduction in size of tubercles near the aperture along with crowded ribs that may be irregular in strength. Secondary ribs may also occur near the aperture (fig. 46A). A complete aperture is not preserved in any of the USGS specimens. Part of the aperture of one adult (USNM 482476, not illustrated), from USGS Mesozoic locality 7201 (fig. 2, loc. 63), with a whorl height of 46 mm, shows crowded and irregular ribs in the last 24 mm of the individual. Tubercles are reduced in size toward the aperture and disappear on the last
two ribs. A microconch (BHMNH 4034), from the Pierre Shale of Carter County, Montana, has the dorsal half of the adult aperture preserved. It follows the trend of the terminal, crowded, flexuous ribs and has a very broad dorsal projection and a slightly convex midflank projection. The crowded ribs and reduced tubercles on several body chambers indicate the mature stage in *Exiteloceras jenneyi jenneyi*. Specimens with these features that have whorl heights at their larger end of as little as 32 mm (for example, unfigured specimens USNM 482477, from loc. 52, and USNM 482490, from loc. D35) are probably macroconchs. Adult specimens that have whorl heights of as much as 74 mm are probably macroconchs (for example, unfigured specimen USNM 482474, from loc. 15).

The complex suture has been illustrated by Whitfield (1880: pl. 15, fig. 5; pl. 16, fig. 9) and Cobban (1970: fig. 3). A typical suture is shown in Figure 40.

**DISCUSSION:** Pathologic specimens are scarce. The largest collection, 61 specimens from USGS Mesozoic locality D304 (fig. 2, loc. 35), does not include a single pathologic specimen. The second largest collection, 48 specimens from USGS Mesozoic locality D2854 (fig. 2, loc. 36), has only one pathologic individual. This specimen (USNM 482479), part of an elliptical limb 75 mm long, has dents along one side of the inner part of the flank as well as a complete loss of ventral tubercles. Two pathologic specimens, however, are present in a much smaller collection of 16 specimens from USGS Mesozoic locality 23053 (fig. 2, loc. 5). One specimen, USNM 482480 (not illustrated), is part of an adult body chamber that has a whorl height of 44 mm. It has a longitudinal groove along the lower part of the flank accompanied by a loss of ribbing in the depression. The other specimen, USNM 482481 (not illustrated), part of an adult body chamber that has a whorl height of 36.5 mm, has a depression on the venter followed by a loss of ornament. Neal Larson (written commun., 1994) observed seven pathologic individuals out of a collection of over 100 specimens collected by Howard Ehrlé from the Pierre Shale of Carter County, Montana (fig. 2, general area of locs. 5–9). Two specimens have a single row of tubercles, three appear to have been broken and rehealed, one has a crease at midflank, and one has a bite that was healed.

**OCCURRENCE:** *Exiteloceras jenneyi jenneyi* is widely distributed in the Pierre Shale around the Black Hills in western South Dakota, northeastern Wyoming, and southeastern Montana (fig. 41). The subspecies also occurs in the Bearpaw Shale in east-central Montana. It has been found at many localities in the two-thirds of Colorado in the Pierre Shale, Mancos Shale, and Iles Formation (Rifle shale unit and Cozzette Sandstone Member). Farther south, it occurs in the Pierre and Lewis shales in northern New Mexico. Kennedy (1992: 174, figs. 14A, C) described two flattened specimens from the Guadalupe Formation of Colombia that he assigned to *E. jenneyi*. One is a juvenile of three subparallel shafts linked by narrowly curved elbows; ribs are rursiradiate and have an index of 6 or 7. The other, a larger elliptical coil, has rursiradiate ribs that have an index of 3 or 4.

*Exiteloceras jenneyi camacki*, new subspecies

**Types:** Holotype USNM 482491 is from the Pierre Shale northeast of Pueblo at USGS Mesozoic locality D1232 in the SE1/4 SE1/4 sec. 23, T. 19 S., R. 64 W., Pueblo County, Colorado (fig. 2, loc. 53). Paratypes are USNM 482486 and 482492–482495 from the Pierre Shale at USGS Mesozoic localities D2619, D13525, D3466, and 1344 (fig. 2, locs. 18, 22, 49, 60, respectively).

**ETYMOLOGY:** For Walter G. Camack, Pueblo, Colorado, who first noted this form in his extensive collections of Pierre Shale ammonites.

**MATERIAL:** About 50 specimens from 25 localities in Montana, Wyoming, and Colorado.

**DIAGNOSIS:** A stout form of *Exiteloceras*
Fig. 49. *Exiteloceras jenneyi camacki*, n. subsp. Side view and two cross sections of the holotype, USNM 482491, locality D1232 (fig. 2, loc. 53). The solid line is the costal section, and the dashed line is the intercostal section. Figure is $\times 1$. 
Fig. 50.  A, B. *Exiteloceras jenneyi camacki*, n. subsp. Paratype, USNM 482495, USGS Mesozoic locality D13525 (fig. 2, loc. 22). Figures are ×1.

*jenneyi* that has a ratio of whorl breadth to whorl height of 0.8 or more.

**DESCRIPTION:** The holotype (fig. 49) is a little more than half of a circular whorl 183 mm in diameter. About two-thirds is phragmocone. At the base of the body chamber, the whorl height is 35.0 mm and the whorl breadth is 30.5 mm (ratio of whorl breadth to whorl height is 0.87). The intercostal section has a broadly rounded dorsum, very broadly rounded flanks, and a more narrowly rounded venter. The costal section is similar, except that the venter is flat. Ornament consists of single, narrow, rursiradial ribs that
are flattened on the venter; the rib index is 6. The suture is like that of *Exiteloceras jenneyi jenneyi*.

Most of the specimens at hand are parts of adult whorls. The few juvenile whorls are fragments of elliptical limbs that have whorl heights of 8.5 mm or more and ratios of whorl breadth to whorl height of 0.8 or more. Ornament on juvenile and adult whorls is like that of *Exiteloceras jenneyi jenneyi*.

The largest specimen in the collections is a part of a macroconch body chamber 71.0 mm high and 59.3 mm wide (ratio of whorl breadth to whorl height is 0.84) (fig. 50). Ribs are rursiradiate, flexuous, and become crowded toward the aperture. Tubercles are small; they are nodate on the earlier part of the specimen and bullate on the later part. The rib index is 7 on the earlier part of the specimen, 10 or 11 on the later part. The complete aperture follows the flexuous form of the ribbing.

**Discussion:** The inflated whorl section of *Exiteloceras jenneyi camacki* separates it from *E. jenneyi jenneyi*, which has a more compressed whorl section. Some individuals of the former have ratios of whorl breadth to whorl height of as much as 0.95 (for example, unfigured paratypes USNM 482492 and 482493, from locs. 18 and 49, respectively).

**Occurrence:** *Exiteloceras jenneyi camacki* occurs low in the zone of *E. jenneyi* and is clearly related to *E. jenneyi jenneyi*. Specimens of *E. jenneyi camacki* have been found at many localities in the Pierre Shale in southeastern Montana, eastern Wyoming, western South Dakota, and eastern Colorado. Specimens from the basal part of the Mount Laurel Sand of Delaware (Cobban, 1970: p. D73, figs. 1g–k, n–r; 3; Kennedy and Cobban, 1997: fig. 9.1–9.10) can be assigned to *E. jenneyi camacki*.

**Family Diplomoceratidae Spath, 1926**

(= Neocrioceratinae Spath, 1953: 17)

**Subfamily Polyptychoceratinae Matsumoto, 1938**

Genus *Oxybeloceras* Hyatt, 1900

**Type Species:** *Ptychoceras crassum* Whitfield, 1877, p. 45, by monotypy.

**Diagnosis:** Two straight shafts in tight contact except for tear-shaped, narrow opening (like the eye of a needle) at the elbow linking shafts. Ornament consists of narrow, sharp ribs that bear two rows of small tubercles. Constrictions lacking; size dimorphism present.

**Discussion:** Hyatt (1900: 588) did not give a definition of *Oxybeloceras*, but merely listed it as “*Oxybeloceras*, gen. nov. Type *O. (Pty.) crassum*, Whitf. sp. Cretaceous,” and placed it in the family Nostoceratidae. The holotype of *Ptychoceras crassum* Whitfield (1880: pl. 16, figs. 3, 4) is an incomplete specimen that consists of two straight shafts about 50–55 mm long joined by an elbow. The older limb has a whorl height of about 6 mm at its smaller broken end, which suggests that much of the earlier parts are missing. Some excellent specimens, collected by Barry Brown (Rapid City, South Dakota) and now in the collections of the R.J.B. Rock Shop (Rapid City), reveal that *Oxybeloceras crassum* attained lengths as much as 170 mm (fig. 54M), and that the smaller limb was still straight at a diameter of 1 mm. Some authors (e.g., Wright, 1957; Ward and Mallory, 1977) regarded *Oxybeloceras* Hyatt (1900) as a synonym of *Solenoceras* Conrad (1860). Matsumoto and Morozumi (1980) regarded *Oxybeloceras* as a subgenus of *Solenoceras*, separating it from the nominate subgenus on the basis of its larger size and absence of constrictions.

**Occurrence:** *Oxybeloceras* is fairly common in the *Baculites stevensoni* and *Exiteloceras jenneyi* zones in the Pierre Shale in Montana, South Dakota, and Colorado.

*Oxybeloceras crassum* (Whitfield, 1877)

**Figures** 51–54

*Ptychoceras crassum* Whitfield, 1877: 45.


*Ptychoceras crassum* Whitfield. Chamberlin and Salisbury, 1906: fig. 417 h, i.

*Ptychoceras (Oxybeloceras) crassum* Whitfield. Grabau and Shimer, 1910: figs. 1464b, c, 1466.
Fig. 51.  A, B. Holotype of Ptychoceras crassum Whitfield, 1877 (from Whitfield, 1880: pl. 16, figs. 3, 4). Figure is ×1.

Ptychoceras crassum Whitfield. Chamberlin and Salisbury, 1914: fig. 470f, g.
Ptychoceras (Oxybeloceras) crassum Whitfield. Grabau, 1921: fig. 1754i, j.
Hamites (Oxybeloceras) crassum Whitfield. Die- ner, 1925: 77.
Oxybeloceras sp. Larson et al., 1997: 57, unnumbered fig.

Types: The holotype, by monotypy, is USNM 12324, from “limestone of the Fort Pierre group, on Old Woman’s Fork, Black Hills” (Whitfield, 1877: 46). It probably came from a limestone concretion in the zone of Didymoceras stevensoni near the top of the lower third of the lower unnamed shale member of the Pierre Shale near Red Bird, Niobrara County, Wyoming. Gill and Cobban (1966) did not record Oxybeloceras in their detailed section of the Pierre Shale near Red Bird, but a collection made later by Cobban from bed 59 of the section (Gill and Cobban, 1966, USGS Mesozoic locality D1940 on p. A55 and on pl. 2) includes Oxybeloceras crassum.

Material: Approximately 300 fragments, chiefly uncrushed internal molds, from about 60 localities in Montana, Wyoming, and Colorado. The largest collections consist of 50 fragments from USGS Mesozoic locality D358 and 35 fragments from USGS Mesozoic locality D359, both from the Rock River Formation near Rock River, Wyoming (fig. 2, locs. 25, 26).

Fig. 52. Part of the fifth from last suture of Oxybeloceras crassum (Whitfield, 1877). USNM 482502. USGS Mesozoic locality D2837 (fig. 2, loc. 40). E is the external lobe, L is the lateral lobe, and the heavy straight line marks the middle of the venter.

Fig. 53. Histogram showing range in diameters of the elbows of 48 specimens of Oxybeloceras crassum (Whitfield, 1877), USGS Mesozoic localities D251, D358, D359, D454, D735, D1364, and D4332.
**Diagnosis:** Earliest whorls of the species probably consist of an open planispiral coil followed by a broadly curved limb. Later whorls consist of two parallel, tightly appressed, straight limbs connected by an elbow. Ornament consists of straight ribs and small tubercles that border the venter. Constrictions seem to be absent.

**Description:** The holotype, the only specimen mentioned by Whitfield, consists of the two straight, parallel limbs and the connecting elbow of an adult (fig. 51) about 48.5 mm long (measurements from a plaster cast). The body chamber includes the larger limb and the elbow. Limbs have subcircular intercostal whorl sections and slightly flattened venters. A small opening shaped like the eye of a needle separates the limbs at the elbow. A pronounced impressed dorsal furrow is present on the larger limb. Ornament consists of strong, sharp, straight ribs; the rib index is 3–3.5. Each rib bears a small, nodate tubercle on each side of the narrower venter. Ribs are prorsiradiate on the smaller limb, rectiradiate on the elbow, and rursiradiate on the larger limb. Ribs weaken on the venter, which they cross transversely. Most of the opposite tubercles on both limbs are connected by weak, looped ribs.

Early growth stages of *Oxybeloceras crassum* are unknown. The bulk of the specimens at hand consists of parts of the two tightly appressed, parallel limbs of adults; the most complete individual known is illustrated in figure 54M. Fragments of smaller, gently curved limbs probably represent a late juvenile growth stage. The broadly curved juvenile limb has a subcircular cross section with a slightly flattened venter. Ornament is of narrow prorsiradiate ribs; the rib index is 4. Each rib bears a small nodate tubercle at the edge of the venter; ribs weaken as they cross the venter transversely.

The two tightly appressed parallel adult limbs can be very long. Some specimens are twice as long as the holotype (fig. 54K, L). The longest specimens at hand have lengths of 90 mm, but longer individuals have been reported. BHMNH 4062, from the zone of *Didymoceras stevensoni* in the Pierre Shale near Newcastle, Wyoming (fig. 2), is incomplete but has a length of 127 mm (fig. 54M); as noted under the generic description others reach 170 mm. Both limbs of *Oxybeloceras crassum* have subcircular whorl sections with slightly flattened venters. A broad, concave dorsal furrow is present on the large limb to accommodate the smaller limb (fig. 54D). Ribs on the smaller limb are narrow, straight, and prorsiradiate; they become rectiradiate on the elbow and then slightly rursiradiate on the larger limb. All ribs except a few near the aperture bear small, nodate to bullate tubercles at the margin of the venter. Well-preserved specimens reveal small, sharp spines that rise from tubercles. Ribs cross the venter transversely, where they are either narrow or broad and looped. The rib index is 3–5.

The aperture follows the form of the ribs. The last two to seven ribs are usually weakened, irregular in height, and crowded. Tubercles weaken greatly and usually become bullate or disappear. The suture is fairly simple and has deeply bifid, triangular-shaped lobes and saddles. Part of a suture is shown in figure 52.

*Oxybeloceras crassum* is dimorphic (fig. 53). Macroconchs are as much as twice the size of microconchs.

**Discussion:** Several species from California described by Anderson (1958) differ considerably from *Oxybeloceras crassum* and may belong to other genera. *Oxybeloceras biconstrictum* Anderson, 1958 (p. 202, pl. 31, fig. 2) is a curved limb with prominent constrictions; *Oxybeloceras petroliense* Anderson, 1958 (p. 203, pl. 56, fig. 1) is a large limb and elbow that has a wide separation; *Oxybeloceras taffi* Anderson, 1958 (p. 203, pl. 51, fig. 6, 6a) is a limb that has eight ribs per whorl height. *Ptychoceras aratus* Conrad, 1874 (p. 455), from “Trout Creek, near Fairplay [Colorado],” probably came from the Pierre Shale and could be a senior synonym of *O. crassum*, but the type was never illustrated and its whereabouts are unknown.

**Occurrence:** *Oxybeloceras crassum* has been found at many localities in Montana, Wyoming, and Colorado, where it is usually associated with *Didymoceras stevensoni*, and less often with *Exiteloceras jenneyi*. A flattened specimen (USNM 482504, not illustrated) consisting of two appressed, straight limbs from the Taylor Group of east-central Texas is probably *O. crassum*. It is from USGS Mesozoic locality 12899 on the right
Fig. 54. *Oxybeloceras crassum* (Whitfield, 1877). A. USNM 482496, USGS Mesozoic locality D1387 (fig. 2, loc. 27). B. USNM 482497, USGS Mesozoic locality D1364 (fig. 2, loc. 16). C, D. USNM 482498, USGS Mesozoic locality D454 (fig. 2, loc. 17). E. USNM 482499, USGS Mesozoic locality D2842 (fig. 2, loc. 38). F. USNM 482500, USGS Mesozoic locality D2630 (fig. 2, loc. 4). G,
Genus *Spiroxybeloceras* Kennedy and Cobban, 1999

**Type Species:** *Ptychoceras meekanum* Whitfield, 1877: 44, illustrated by Whitfield, 1880: pl. 16, figs. 1, 2, from the Pierre Shale, Wyoming.

**Diagnosis:** Heteromorph ammonites characterized by a loose planispiral juvenile growth stage and an adult stage of two parallel shafts barely in contact. Ornament of narrow, sharp ribs that bear small, pointed tubercles bordering the narrow venter (fig. 56).

**Discussion:** Large collections of *Spiroxybeloceras* now at hand reveal that the shell consists of a minute ammonitella whorl and two open planispiral whorls in contact followed by a broadly curved limb merging into the older of the two straight shafts (fig. 56). The only previously published photographs of complete Western Interior *Spiroxybeloceras* are those of Hirsch (1975: fig. 10), Kennedy and Cobban (1993b: fig. 10A), and Larson et al. (1997: 58). Several specimens of a fine-ribbed *Spiroxybeloceras* were figured by Lewy (1967: 170, pl. 3) as *Solenoceras humei humei* (Douvillé, 1928) and *Solenoceras humei densicostata* Lewy from the upper Campanian Mishash Formation in Israel. These specimens show parts of the outer planispiral whorl that merges into the older of the two straight shafts.

Reference of *Spiroxybeloceras* to Diplomoceratidae rather than Nostoceratidae is made with no great confidence, given the uncertainty surrounding its phylogenetic relationships.

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Spioxybeloceras meekanum (Whitfield, 1877)

Figures 55–57

Ptychoceras meekanum Whitfield, 1877: 44.
Ptychoceras meekanum Whitfield. Whitfield, 1880: 457, pl. 16, figs. 1, 2.
Oxybeloceras meekanum (Whitfield). Hyatt, 1900: 588.
Ptychoceras meekanum Whitfield. Grabau, 1921: fig. 1754h.
Oxybeloceras sp. Lauginiger, 1988: pl. 6, fig. 3.
Oxybeloceras meekanum (Whitfield). Kennedy and Cobban, 1993b: 143, fig. 10A.
Oxybeloceras meekanum (Whitfield, 1877). Kennedy et al., 1995: pl. 5, figs. 15, 16.
Oxybeloceras meekanum (Whitfield, 1877). Larson et al., 1997: 58, two unnumbered figs.

Types: The holotype is USNM 12279, the original of Whitfield, 1877: 44; 1880: 457, pl. 16, figs. 1, 2. According to Whitfield (1877: 45), the specimen came from “limestone of the Fort Pierre group, on Beaver Creek, Black Hills.” The specimen probably came from a limestone concretion in the upper part of the Monument Hill Bentonitic Member of the Pierre Shale in the Beaver Creek drainage near Newcastle, Weston County, Wyoming. Spioxybeloceras meekanum is known only from the zone of Dymoceras cheyennense, which lies in the upper part of the Monument Hill Member (Gill and Cobban, 1966: pl. 4).

Material: About 150 fragments, all internal molds, from about 30 localities. The largest collection consists of 25 fragments of juveniles from USGS Mesozoic locality D68 near Denver, Colorado (fig. 2, loc. 43).

Diagnosis: A fairly small species of Spiroxybeloceras characterized by an initial open planispiral coil and short body chamber. A short, broadly curved limb connects the planispiral coil to the body chamber.

Description: The holotype (figs. 55, 57H) consists of two short, parallel limbs in contact and part of the uncoiled, broadly curved limb. The entire specimen is about 48.3 mm long (measurements from a plaster cast). The uncoiled limb has a subcircular whorl section with a slightly flattened venter, whereas the smaller of the straight limbs has a slightly depressed whorl section and a more flattened venter. The larger straight limb has a depressed whorl section with both the venter and dorsal flattened. A narrow, tear-shaped opening lies in the elbow that connects the two straight limbs. Ribs are narrow, single, straight, and prorsiradiate on the uncoiled limb and on the smaller of the straight limbs. Ribs become rectiradiate on the middle of the elbow and then slightly rursiradiate on the remainder of the elbow and on the larger limb. All ribs bear small, nodate tubercles. Tubercles on the smaller of the straight limbs are connected by very weak transverse ribs. Transverse ribs are strong on the larger limb. Ribs on the venter of the limbs are spaced such that the rib index is 3.

A complete individual is present in the collections of the Black Hills Museum of Natural History (fig. 57I). The specimen has an ammonitella followed by an open planispiral of two whorls, barely in contact. The ammonitella is free from the rest of the coil. The rest of the first whorl then barely touches the second whorl. Ribs first appear about a quarter of a whorl beyond the ammonitella. These ribs are at first rectiradiate and then become rursiradiate for the remainder of the coil. A short straight limb extends from the coil, bends slightly, and merges into the smaller of two final straight limbs. A high rib lies near the aperture.
Several specimens in the USGS collections retain the initial coiled growth stage (fig. 56). Diameters of the coil range from 11.5 to 12.00 mm.

Whitfield’s (1880: pl. 16, fig. 1) illustration of the holotype shows slight curvature of the larger parallel limb. In specimens examined by us the limb is straight, slightly curved as in Whitfield’s illustration, or even a little more curved.

The short body chamber begins on the smaller parallel limb at the beginning of the elbow or a rib or two before it. Several specimens have the aperture preserved. Usually a high, nontuberculate rib is followed by a weak, nontuberculate rib, and then by the aperture (fig. 56). Dimorphism cannot be conclusively demonstrated from the material at hand.

Deeply bifid lateral and umbilical lobes that have a triangular shape characterize the suture (fig. 55). The external lobe is rather rectangular; the internal lobe is small and pointed.

Discussion: Solenoceras himei himei (Douville, 1928), as described and illustrated by Lewy (1967: 170, pl. 3, figs. 1–3), has a short body chamber and a juvenile planispiral coil similar to that of Spiroxybeloceras meekanum, but the ribbing is much denser. Douville’s species seems better assigned to Spiroxybeloceras. Hamites interruptus Schlüter, 1872 (p. 105, pl. 32, figs. 8, 9; holotype refurged by Klinger, 1982: fig. 8F, G) is known from specimens that consist of two parallel limbs connected by a narrow, curved section. The limbs of the holotype are more widely spaced than those of typical S. meekanum. Additional material may reveal that Schlüter’s species is a species of Spiroxybeloceras.

Occurrence: Spiroxybeloceras meekanum seems to be confined to the upper Campanian zone of Didymoceras cheyennense. Specimens of S. meekanum have been found in the Pierre Shale in southeastern Montana, western South Dakota, eastern Wyoming, northwestern Nebraska, north-central and eastern Colorado, and northeastern New Mexico. The species has also been collected from the Mount Laurel Sand of Delaware (Kennedy and Cobban, 1994). Petters (1955: 216, 224) reported the species from Colombia, as Solenoceras meekanum.

Genus Solenoceras Conrad, 1860

Type Species: Hamites annulifer Morton, 1841: 109, 1842, p. 213, pl. 11, fig. 4 by the subsequent designation of Conrad, 1860: 284.

Diagnosis: A small genus that consists of two straight shafts in tight contact with the
old shaft extending, straight or slightly curved, beyond the aperture and arising from a minute ammonitella coil (fig. 66). With the exception of a very small tear-shaped opening at the elbow, the younger shaft has a prominent impressed dorsal furrow resulting from growth of that shaft over the dorsum of the older shaft. Constrictions may or may not be present on both shafts, but the aperture is usually preceded by a conspicuous constriction bounded by high ribs (figs. 58, 66). Ornament consists of narrow, straight, closely spaced ribs that are prorsiradiate on the older shaft and rursiradiate on the younger shaft. Each rib ordinarily bears a minute tubercle on each side of the venter. Size dimorphism is present.

**Discussion:** Morton’s type specimen, well illustrated by Reeside (1962, pl. 70, figs. 8–10), is a small densely ribbed body chamber 21 mm long that begins at the elbow. Conspicuous constrictions are present in the middle of the elbow, in the middle of the shaft, and at the aperture; at the aperture the constriction is bounded by high ribs. Tubercles bordering the venter are barely visible.

The early growth stages of *Solenoceras* have not been previously described or illustrated. The restoration shown in figure 66 is based mainly on juvenile growth stages of specimens found in calcareous concretions in the upper Campanian *Didymoceras stevensoni* zone in the Rock River Formation of Wyoming.

*Solenoceras* differs from *Oxybeloceras* in possessing constrictions and in having the early growth stages in the form of a gently curved shaft that originates from a tiny initial coil.

**Occurrence:** *Solenoceras* has been found in the Western Interior only in the middle and upper Campanian. It occurs in the zones of *Baculites gregoryensis* and *Baculites scotti* in the Pierre Shale in South Dakota; in the *Didymoceras stevensoni* zone in the Pierre Shale in Colorado, Wyoming, and Montana; in the *Didymoceras nebrascense* zone in the Bearpaw Shale in Montana and in the Pierre Shale in South Dakota and Colorado; in the *Exiteloceras jenneyi* zone in the Pierre Shale in Montana, South Dakota, and Colorado; and in the *Baculites reesidei* zone in the Pierre Shale in Colorado, Wyoming, and Montana. *Solenoceras* has been recorded from Arkansas, Texas, Tennessee, Mississippi, Georgia, and California, as well as from Spain? (Martinez, 1982), Italy (Giudici and Pallini, 1993), Belgium (Kennedy, 1993), Angola (Haughton, 1925), Nigeria? (Zaborowski, 1985), Israel? (Lewy, 1969), Egypt? (Hamama and Kassab, 1990), and Japan (Matsumoto and Morozumi, 1980).

*Solenoceras bearpawense*, new species

Figures 58–60, 61G–Q, 62

*Solenoceras* n. sp. Gill et al., 1972: 95.

*Solenoceras* sp. Larson et al., 1997: 47, two unnumbered figs.

**Types:** The holotype is USNM 482510,
from a limestone concretion in the Didymoceras nebrascence zone of the Bearpaw Shale at USGS Mesozoic locality D2629 in the NE1/4 sec. 31, T. 10 N., R. 36 E., Rosebud County, Montana. Paratypes are USNM 482511–482514, from the same locality; USNM 482515, from the Pierre Shale at USGS Mesozoic locality D1421 (fig. 2, loc. 13); USNM 482516, from the Pierre Shale at USGS Mesozoic locality D1421 (fig. 2, loc. 12); USNM 482517, from the Pierre Shale at USGS Mesozoic locality D1421 (fig. 2, loc. 55); and USNM 482518–482520, from the Pierre Shale at USGS Mesozoic locality D3935 (fig. 2, loc. 61).

**ETYMOLOGY:** For the Bearpaw Shale of Montana.

**MATERIAL:** About 275 fragments, mostly uncushioned internal molds, from 25 localities. The largest collection contains about 100 fragments from limestone concretions in the Bearpaw Shale at USGS Mesozoic locality D2629 in Rosebud County, Montana (fig. 2, loc. 3).

**DIAGNOSIS:** A slender species of Solenoceras with periodic constrictions bounded by flared ribs on the smaller limb, weakened ornament or loss of ornament on the elbow, and a finely ribbed larger limb (fig. 58).

**DESCRIPTION:** The holotype (fig. 61M, N) consists of two tightly appressed limbs 43.0 mm long, connected by a narrowly rounded elbow, 10.2 mm in diameter. The body chamber occupies the elbow and larger limb. The larger limb, which lacks its adapertural end, has a maximum costal height of 6.2 mm and width of 5.7 mm. The smaller limb has a circular cross section at the smaller end, where the diameter is 3.8 mm. Three or four very weak constrictions bounded by high ribs are present on the smaller limb. Ribs are prorsiradiate and rather weak on the smaller limb, where the rib index is 4; they bear minute nodate tubercles that border the narrow venter. Opposite tubercles are connected across the venter by very weak transverse ribs. Ornament weakens and almost disappears on the larger end of the elbow. Ribs and tubercles rejuvenate on the larger limb; ribs are rursiradiate, with a rib index of 6. Ribs are narrow on the flanks; they are straight, rounded, and narrower than the interspaces. Each rib bears a very small, nodate tubercle at the margin of the venter. Opposite tubercles are connected by transverse flattened ribs.

Most specimens in the collections resemble the holotype in size and ornament. Ribbing is weak on the smaller limb but strong on the larger limb, where the rib index is 5, occasionally 4 or 6. Well-preserved specimens have three minute longitudinal siphonal ridges on the elbow and adjoining part of the larger limb. Constrictions are widely spaced on the smaller limb, commonly at every ninth rib; they are occasionally present at every fourth to sixth rib on the larger limb.

The smallest limbs in the collections are straight to slightly curved, circular in whorl section with diameters as small as 0.8 mm (USNM 482517, not illustrated) and smooth except for periodic constrictions. The largest
specimen (USNM 482516, not illustrated) in the collections has a diameter of 7.8 mm at the aperture. The final rib or two becomes nontuberculate and irregular in height. The aperture may be preceded by a short area that has striae following the course of the ribs. A small, broad, convex projection is present on the dorsum.

Dimorphism cannot be definitely demonstrated. Diameters of the 25 measurable elbows present in the collection from USGS Mesozoic locality D1422 (fig. 2, loc. 13) are summarized in figure 59. Two body chambers in the BHMNH collection from the Didymoceras nebrascense zone of the Pierre Shale southeast of Rapid City, South Dakota, have body chambers 78 and 88.6 mm long (N. Larson, written commun., 1994).

The suture is fairly simple (fig. 60). The external lobe is rectangular, the lateral lobe is deeply bifid; the saddle that separates these lobes is bifid and about the size of the lateral lobe.

DISCUSSION: Solenoceras bearpawense, n. sp., is the oldest known species of the genus in the Western Interior. The species is closely
related to *Solenoceras bembense* Haas, 1943 (p. 11, figs. 4, 14) from Angola. The holotype of the African species, represented by the smaller of the two parallel limbs, has five ribs per limb height and a constriction bordered by a strong apical rib. The ribbing of the holotype of *S. bembense* is a little denser and stronger than that of the smaller limb of *S. bearpawense*. Of the American species, *S. bearpawense* is nearest to *Solenoceras texanum* (Shumard, 1861: 189), from which it differs in having more inflated limbs. The smaller limb of both species is weakly ribbed and bears constrictions. *S. texanum* is present, however, in the Western Interior at a higher level (zones of *Baculites cuneatus* and *Baculites reesidei*). *Solenoceras mexicanum* Anderson, 1958 (p. 211, pl. 72, fig. 8) also has a weakly ornamented smaller limb, but constrictions seem to be absent, and the California species is smaller. Other described species of *Solenoceras* differ considerably from *S. bearpawense*.

**Occurrence:** *Solenoceras bearpawense* seems to range throughout the upper Campanian zone of *Didymoceras nebrascense* (fig. 62). Specimens of *S. bearpawense* have been collected from the lower part of the Bearpaw Shale in east-central Montana (Gill et al.; 1972: 95, *Solenoceras*, n. sp., of unit 49), and from the middle part of the Pierre Shale in southeastern Montana, western South Dakota, and eastern Colorado. Other specimens have been found in the Mesaverde Formation (below the Teapot Sandstone Member) in east-central and south-central Wyoming and in the Mancos Shale (below the Cozzette Sandstone Member of the Iles Formation) in west-central Colorado. The species also occurs in the Lewis Shale in the eastern side of the San Juan Basin in northwestern New Mexico (N. Larson, written commun., 1994).

*Solenoceras larimerense*, new species

Figsures 61A–F, 63, 64


*Solenoceras mortoni* (Meek and Hayden). Scott and Cobban, 1986b: map explanation.
Types: The holotype is USNM 482521, from a sandstone concretion in the Terry Sandstone Member (Exiteloceras jenneyi zone) of the Pierre Shale at USGS Mesozoic locality D304 near Fort Collins, Larimer County, Colorado (fig. 2, loc. 35). Paratypes are USNM 482522–482524, from the same locality; USNM 482525 and 482526 from the Terry Sandstone Member at USGS Mesozoic locality D303 (fig. 2, loc. 34); USNM 482527, from the Pierre Shale at USGS Mesozoic locality D803 (fig. 2, loc. 44); USNM 482528, from the Pierre Shale at USGS Mesozoic locality D986 (fig. 2, loc. 32); and USNM 482529, from the Pierre Shale at USGS Mesozoic locality D8629 (fig. 2, loc. 48).

Etymology: From Larimer County, Colorado.

Material: Twenty specimens, all incomplete internal molds.

Diagnosis: A very small species of Solenoceras with three or four ribs per limb height. Constrictions rare, but may occur on either limb (fig. 63).

Description: The holotype (fig. 61C) consists of two tightly appressed limbs connected by a narrow elbow 4.4 mm in diameter. The total length of the specimen is 20.7 mm. The smaller limb is broken off at a limb height of 1.3 mm, where the whorl section is circular. Ornament of this limb consists of single, straight, prorsiradiate ribs; the rib index is 4; each rib bears a minute, nodate tubercle at the margin of the venter. Ribs greatly weaken on the elbow, but tubercles remain conspicuous there. About 13.3 mm of the larger limb is preserved; the adoral end has a height of 2.8 mm, although it is somewhat crushed laterally. Ribs are rectiradiate on the elbow and rursiradiate on the larger limb; they are single, narrow, and straight; the rib index is 4. The body chamber occupies the larger limb and elbow.

Seven paratypes (USNM 482522, 482523, 482524a–e), from USGS Mesozoic locality D304 (fig. 2, loc. 35), have elbow diameters of 4.7, 4.9, 5.2, 5.4, 5.5, 5.5, and 5.6 mm. Smaller limbs have whorls about as high as wide; they have broadly rounded dorsums, well-rounded flanks, and slightly flattened, narrow venters. Larger limbs have whorls about as high as wide, and have prominent impressed dorsal furrows. Three paratypes (USNM 482525, 482526a, b), from a nearby locality (D303), have elbow diameters of 4.7, 4.9, and 5.0 mm. Two paratypes (USNM 482527a, b), from another locality (D803), have elbow diameters of 4.8 and 5.0 mm. One of these specimens has two constrictions on the larger limb, each bounded by high adoral and adapical ribs.

The suture of Solenoceras larimerense, n. sp., is very simple. The external and lateral lobes and adjoining saddles are bifid, without further subdivisions (fig. 64).

Discussion: The species differs from Solenoceras bearpawense in its much smaller size and slightly sparser ribbing. Solenoceras mortoni (Meek and Hayden, 1857) (p. 134) is slightly larger and has occasional constrictions; Solenoceras mexicanum Anderson, 1958 (p. 211, pl. 72, fig. 8), likewise, is a little longer.

Occurrence: Solenoceras larimerense seems to be confined to the upper Campanian zone of Exiteloceras jenneyi. Most specimens are from the Terry Sandstone Member of the Pierre Shale in the Fort Collins area in northern Colorado. The species has also been found with Exiteloceras jenneyi jenneyi in the Pierre Shale near Red Bird, Niobrara County, Wyoming (fig. 2, loc. 22).

Solenoceras elegans, new species

Figures 61R–HH, 65–67

Solenoceras, n. sp. Gill et al., 1970: 22, 23.

Types: The holotype is USNM 482530, from the Rock River Formation at USGS Mesozoic locality D1387 in the NW ¼ sec. 16, T. 20 N., R. 76 W., Albany County, Wyoming (fig. 2, loc. 27). Paratypes are USNM 482531–482538, 482823–482826, from the same locality, and 482539, from USGS Mesozoic locality D359 (fig. 2, loc. 26).

Etymology: Latin, elegans, fine.

Material: About 200 well-preserved fragments from the type locality plus about 30 fragments from other localities.

Diagnosis: A long, slender species of Solenoceras with a few constrictions near the adapical end and one near the aperture. Ribs are usually closely spaced with a rib index of 5.

Description: The holotype (fig. 61DD)
Fig. 65. Histogram showing range in diameters of the elbows of 45 specimens of *Solenoceras elegans*, n. sp., USGS Mesozoic locality D1387 (fig. 2, loc. 27).

consists of two tightly appressed, slightly curved limbs 69 mm long, connected by a narrow elbow 9.6 mm in diameter. Owing to cover of nacreous shell material on nearly all of the smaller limb, the position of the base of the body chamber is not recognizable. The small end of the smaller limb is broken off at a limb height of about 2 mm. The height of the larger limb is about 6.5 mm at the aperture. Both limbs have stout cross sections. Ribs are straight, narrow, and single; each bears a small nodate tubercle at the margin of the flattened venter. Short, sharp spines are preserved near the aperture, where they arise from tubercles. Ribs are prorsiradiate on the smaller limb and on the older part of the elbow; they are rectiradiate on the middle of the elbow, and slightly rursiradiate on the younger part of the elbow and on the larger limb. The rib index is 5. The aperture is bordered by a thin rib.

Forty-five specimens from USGS Mesozoic locality D1387 have their elbows preserved. The diameters of the elbows are summarized in figure 65. The bulk of the specimens have elbow diameters from 8 to 10 mm.
One of the smallest individuals (USNM 482823, not illustrated) in the collection is a limb 30.5 mm long that has terminal whorl heights of 0.4 and 2.3 mm. Beginning at the small end, the limb forms a gentle curve for about 8 mm and then becomes straight for the rest of the limb. Given the small height of the limb at its smaller end, only a few millimeters of limb and ammonitella can be missing. The ornament is lacking except for a few widely spaced constrictions. Another juvenile limb (USNM 482824, not illustrated), 5.5 mm long, that arises from the ammonitella, is 0.5 mm high at the larger end and forms a gentle curve. This limb is also smooth except for a few weak constrictions. These specimens as well as other very small limbs in the collection (USGS Mesozoic locality D1387) allow restoration of the early growth stages of *Solenoceras elegans* shown in figure 66.

The ornament of the specimens from USGS Mesozoic locality D1387 (fig. 61R–CC, EE–GG) is much like that of the holotype. Ribs are fairly strong, narrow, and closely spaced, and cross the venter transversely, where some may be looped between opposite tubercles. The ornament remains strong on the elbow.

Several specimens have the aperture preserved. A constriction is bordered by a high adoral rib, followed by a weak rib, and then by the aperture (fig. 66). The aperture has the form of the ribs and a broad convex dorsal projection.

The suture is typical of the genus. The lobes and saddles are bifid and of nearly equal size except for the narrow, trifid internal lobe (fig. 67).

**DISCUSSION:** *Solenoceras elegans,* n. sp., has a long body chamber and ribbing much like that of *Solenoceras bearpawense,* n. sp., but *S. elegans* lacks constrictions on the small limb. The long body chamber and density of ribs of *Solenoceras texanum* (Shumard, 1861), as illustrated by Stephenson (1941: pl. 77, figs. 4, 5), resemble those of *S. elegans,* but the Texas species has a rectangular cross section as well as constrictions on the small limb.

**OCCURRENCE:** *Solenoceras elegans* is fairly common in part of the Rock River Formation in southeastern Wyoming, where the species is associated with *Didymoceras stevensoni.* At many localities in Colorado, *S. elegans* ranges upward into the zone of *Exiteloceras jenneyi.* BHMNH has 10 specimens collected by Howard Ehrle from the *D. stevensoni* and *E. jenneyi* zones of the Pierre Shale of Carter County, Montana (N. Larson, written commun., 1994).

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Ward, P., and W. Orr

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Wiedmann, J.

Wright, C. W.


Zaborski, P.M.P.
APPENDIX 1

**Fossil Localities Mentioned in Text**

Prefix D indicates Denver Mesozoic locality numbers; all others are Washington, D.C. Mesozoic locality numbers.

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<th>Locality Number</th>
<th>Collector, year of collection, description of locality, stratigraphic assignment</th>
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APPENDIX 1. Fossil Localities Mentioned in Text continued

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<td>D85</td>
<td>W.A. Cobban, 1954. NE¼ sec. 12, T. 33 N., R. 76 W., Converse County, Wyo. Mesaverde Formation, from silty concretions 25–27 m above Parkman Sandstone Member.</td>
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<td>D251</td>
<td>W.A. Cobban, 1954. SE¼ sec. 1, T. 33 N., R. 76 W., Converse County, Wyo. Mesaverde Formation, from silty concretions 8–12 m below base of Teapot Sandstone Member.</td>
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<td>D1794</td>
<td>G.R. Scott and W.A. Cobban, 1958. SE¼ sec. 4 and NW¼ sec. 9, T. 4 N., R. 69 W., Larimer County, Colo. Pierre Shale, from gray limestone concretions in a sandy unit above the Terry Sandstone Member.</td>
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**APPENDIX 1. Fossil Localities Mentioned in Text continued**

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<td>46 D7028</td>
<td>V.L. Freeman and W.A. Cobban, 1969. SW¼ sec. 17, T. 9 S., R. 85 W., Pitkin County, Colo. Iles Formation, from phosphatic nodules at top of Cozzette Sandstone Member equivalent.</td>
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<td>62 D625</td>
<td>W.A. Cobban, 1955. 1.9 km southeast of Wild Horse, Cheyenne County, Colo. Pierre Shale, from unit of ferruginous concretions.</td>
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<td>63 7201</td>
<td>W.T. Lee, 1911. Bluff about 0.6 km north of Dulce, N. Mex. Lewis Shale, about 150 m below top.</td>
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