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A new species of *Hoploscaphites* (Ammonoidea: Ancyloceratina) from cold methane seeps in the Upper Cretaceous of the U.S. Western Interior

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ABSTRACT

We describe *Hoploscaphites gilberti*, n. sp. (Ammonoidea: Ancyloceratina), from the Upper Cretaceous (middle-upper Campanian) Pierre Shale spanning the zones of *Baculites scotti* and *Didymoceras nebrascense* in Colorado, Wyoming, Montana, and South Dakota. This species is strongly dimorphic and is characterized by a compressed whorl section, with a rounded to elongate outline in lateral view. The apertural angle is approximately 50° in macroconchs. The body chamber is ornamented with fine flexuous ribs, umbilicolateral bullae, and ventrolateral tubercles. *Hoploscaphites gilberti*, n. sp., most closely resembles *H. gilli* Cobban and Jeletzky, 1965, but differs from this species in several important features: (1) the flanks of the body chamber are nearly subparallel rather than steeply convergent toward the venter, (2) the ventrolateral tubercles are larger and more numerous, and (3) the ribs are more widely spaced. *Hoploscaphites gilberti*, n. sp., is abundant at “tepee buttes” in the Pierre Shale, which are now interpreted as cold methane seeps.

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INTRODUCTION

Recent publications have stressed the importance of cold methane seeps as habitats in the Late Cretaceous Western Interior Seaway (Kauffman et al., 1996; Bishop and Williams, 2000; Kiel et al., 2012; Landman et al., 2012; Larson et al., 2013). These seeps are preserved as carbonate mounds and were originally called “tepee buttes” because of their resemblance to the tepees or lodges of the Shoshone and other American Indians (Gilbert and Gulliver, 1895; Gilbert, 1896). When these deposits were first documented in the Pierre Shale of eastern Colorado, their origin was unclear. Gilbert and Gulliver (1895) suggested, among other theories, that these deposits formed due to favorable conditions on the sea floor leading to the long term accumulation of lucinid bivalves. Today, these deposits have been interpreted as the sites of cold methane seeps based on the geochemical signatures of the carbonate matrix and associated fossils (Landman et al., 2012).

In this paper we describe a new species of *Hoploscaphites* (Ammonoidea: Ancyloceratina) from cold methane seep deposits in the Upper Cretaceous (Campanian) Pierre Shale of Colorado, Wyoming, South Dakota, and Montana. *Hoploscaphites gilberti*, n. sp., is strongly dimorphic, and is characterized by a compressed whorl section, with a rounded to elongate outline in lateral view. It is ornamented with fine flexuous ribs and umbilicolateral bullae and ventrolateral tubercles. It most closely resembles *H. gilli* Cobban and Jeletzky, 1965, but differs from this species in the shape of the whorl cross section and details of the ornamentation. Notably, the ribs are more widely spaced and the ventrolateral tubercles are larger and more numerous in *H. gilberti*, n. sp., than in *H. gilli*. The abundance of *H. gilberti*, n. sp., at cold methane seep deposits and its relative rarity elsewhere in the basin raises the question of the role of seeps in the distribution and evolution of ammonites.

GEOLOGIC SETTING

During the Late Cretaceous, a broad seaway extended from Mexico to the western Canadian Arctic (Gill and Cobban, 1966; Kauffman and Caldwell, 1993). The western margin of this seaway was bordered by a north-south trending unstable cordillera, whereas the eastern margin was formed by the low-lying stable platform of the eastern part of the conterminous United States and Canada (Cobban et al., 1994). The position of the western shoreline of the Western Interior Seaway during the late middle Campanian is shown in figure 1. The shoreline trended north-south across the eastern one-third of Montana and Wyoming and formed an embayment across Colorado that extended into eastern Utah. The water depth at the time is difficult to establish, but recent studies have suggested that the entire seaway was less than 100 m deep (Gill and Cobban, 1966; Kauffman, 1967; Howe, 1987; Kauffman and Caldwell, 1993; Kauffman et al., 1996; Sageman and Arthur, 1994).

The sedimentary record of the seaway contains a rich molluscan fauna that is useful in subdividing the Upper Cretaceous strata of this region into fine biostratigraphic zones. This zonation has been integrated with radiometric dates thanks to the presence of interbedded bentonites. We follow the standard zonation of Cobban et al. (2006) as shown in table 1, in which the Campanian stage is subdivided into three substages. *Hoploscaphites gilberti*, n. sp.,

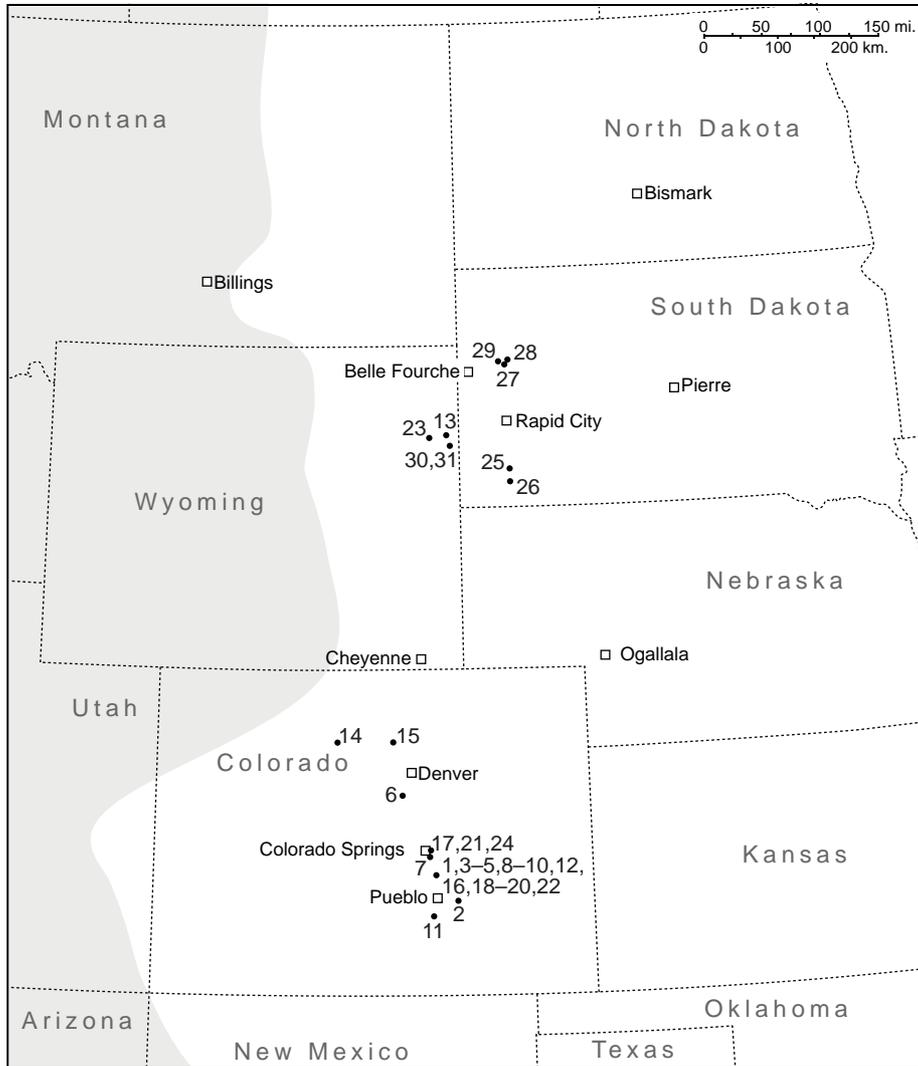


FIG. 1. Map of the middle Campanian *Baculites scotti* Zone showing the shoreline along the western margin of the Western Interior Seaway (reproduced from Cobban et al., 1994). The numbered dots indicate USGS and AMNH localities cited in the text, as listed in the appendix.

occurs in the *Baculites scotti* and *Didymoceras nebrascense* zones, which range from the upper middle to lower upper Campanian, approximately 75 million years ago. Localities mentioned in the text are illustrated in figure 1 and described in the appendix. Most localities occur along the Front Range of the Rocky Mountains in Colorado, and on the flanks of the Black Hills in Wyoming, South Dakota, and Montana.

METHANE SEEPS

Tepee buttes were first described by Gilbert and Gulliver (1895) along the Front Range of the Rocky Mountains in Colorado (fig. 2A). They appear in the landscape as conical hills or

TABLE 1
Upper Cretaceous (Campanian) ammonite biostratigraphy of the U.S. Western Interior showing the zones of *Baculites scotti* and *Didymoceras nebrascense* (Cobban et al., 2006).
 The absolute ages are derived from $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of bentonites containing sanidines.

Stage		U.S. Western Interior Ammonite Zones	Age (Ma)
Campanian	upper	<i>Baculites eliasi</i>	71.98 ± 0.31
		<i>Baculites jenseni</i>	
		<i>Baculites reesidei</i>	72.94 ± 0.45 ¹
		<i>Baculites cuneatus</i>	
		<i>Baculites compressus</i>	73.52 ± 0.39
		<i>Didymoceras cheyennense</i>	74.67 ± 0.15
		<i>Exiteloceras jenneyi</i>	75.08 ± 0.11 ²
		<i>Didymoceras stvensoni</i>	
		<i>Didymoceras nebrascense</i>	75.19 ± 0.28
	middle	<i>Baculites scotti</i>	75.56 ± 0.11, ³ 75.84 ± 0.26
		<i>Baculites reduncus</i>	
		<i>Baculites gregoryensis</i>	
		<i>Baculites perplexus</i>	
		<i>Baculites sp.</i> (smooth)	
		<i>Baculites asperiformis</i>	
		<i>Baculites maclearni</i>	
		<i>Baculites obtusus</i>	80.58 ± 0.55 ²
	lower	<i>Baculites sp.</i> (weak flank ribs)	
		<i>Baculites sp.</i> (smooth)	
		<i>Scaphites hippocrepis III</i>	
		<i>Scaphites hippocrepis II</i>	81.86 ± 0.36
<i>Scaphites hippocrepis I</i>			
		<i>Scaphites leei III</i>	

¹ $^{40}\text{Ar}/^{39}\text{Ar}$ on sanidine as corrected by Baadsgaard et al. (1993).

² Low in zone.

³ Izett et al. (1998).

mounds usually forming irregular clusters. They are composed of limestone, up to 60 m in diameter, and 10 m in height (fig. 2). They are widespread in the Upper Cretaceous Pierre Shale of the U.S. Western Interior, where they are known from central Montana to south-central Colorado, and from the Front Range of the Rocky Mountains to western Kansas (Kauffman et al., 1996; Bishop and Williams, 2000; Shapiro and Fricke, 2002; Metz, 2010). They range in age from middle Campanian to early Maastrichtian. Similar deposits have also been reported from the upper Cenomanian Tropic Shale of Utah (Kiel et al., 2012).

Although the morphology of tepee buttes varies, most buttes consist of a limestone “core” with branching pipe-like conduits. The limestone is nodular and vuggy and contains large concentra-



FIG. 2. Tepee buttes in the Pierre Shale of Colorado, Wyoming, and South Dakota. **A.** Tepee butte along the Front Range of Colorado, as illustrated by Gilbert (1896: pl. 67). **B.** Overview of tepee buttes at AMNH loc. 3494, Weston County, Wyoming. Photo by S. Klofak. **C.** Close-up of tepee butte at AMNH loc. 3494, Weston County, Wyoming. Photo by M. Garb. **D.** Close-up of tepee butte at AMNH loc. 3344, Butte County, South Dakota, with three of the authors for scale. Photo by B. Brown. **E.** Tepee butte near AMNH loc. 3344, Butte County, South Dakota. The shale surrounding the limestone core of the tepee butte has weathered away, exposing the core. Photo by B. Brown. **F.** Macroconch of *Hoploscaphites gilberti*, n. sp., AMNH loc. 3494, Weston County, Wyoming. Photo by M. Garb.

tions of lucinids forming a coquinite. The isotopic composition of the carbonate cements is extremely depleted in $\delta^{13}\text{C}$. Kauffman et al. (1996) reported that the $\delta^{13}\text{C}$ of cements in seep deposits from Colorado ranges from -45 to -40‰. Similarly negative values have been documented from Cretaceous seeps in the Canadian Arctic (Beauchamp and Savard, 1992). Recently, Landman et al. (2012) reported values of -47 to -11.5‰ for carbonate cements from a seep in the Upper Cretaceous of South Dakota. Such negative values indicate that these sites represented cold methane seeps. The carbon was derived from bacterially mediated methane oxidation, which increased the concentration of dissolved inorganic carbon (DIC) and promoted the authigenic precipitation of carbonate minerals resulting in broad limestone platforms. The source of the methane was probably nutrient rich brines or connate waters in the Pierre Shale and, possibly, the underlying Niobrara Formation (Kauffman et al., 1996).

The methane seeps support an abundant and diverse community including ammonites (Landman et al., 2012; Larson et al., 2013), bivalves, notably inoceramids and aggregations of chemosymbiotic-harboring lucinids, gastropods, crinoids (Hunter et al., in press), echinoids, crabs (Bishop and Williams, 2000), sponges, tube worms, chemosynthetic bacteria, foraminifera, and radiolarians. Howe (1987) reported a diversity of approximately 30 molluscan species at single sites from the Campanian of Colorado. It is possible that the diversity of organisms is higher at seeps where the carbonate deposits (lithostromes) are more extensively developed because such deposits provide additional habitats for organisms like crinoids that require hard substrates for attachment (Handle and Landman, 2012; Hunter et al., in press). In comparison, the sea floor immediately adjacent to the seeps is usually more depauperate, and may have been characterized by dysoxic water conditions.

Ammonites formed an integral part of the methane seep community. Landman et al. (2012) investigated the role of ammonites at a seep from the *Didymoceras cheyennense* Zone of the Pierre Shale in western South Dakota. The ammonites are very well preserved at this site and retain their original nacreous microstructure, thus permitting an analysis of the carbon isotopic composition of the shells. The $\delta^{13}\text{C}$ values of the ammonites range from -13.71 to 0.68‰. These values are lighter than those in nonseep specimens from age-equivalent rocks elsewhere in the basin (-1.75 to 3.42‰). The isotopic composition of a single specimen through ontogeny also shows consistently light values. In addition, ammonites at this seep display lethal injuries indicating that they were preyed upon and died at the site. According to this study, the ammonites, although mobile, apparently remained at the seep or seep field throughout their lives. They may have feasted on the abundant local zooplankton, as suggested by the study of the buccal apparatus of *Baculites* by Kruta et al. (2011).

The ammonites at the seeps in the present study, including *Hoploscaphites gilberti*, n. sp., are not well enough preserved to analyze the isotopic composition of their shells. However, both juveniles and adults of *H. gilberti*, n. sp., are present, suggesting that the animals lived at the seeps throughout their lives. Some of the specimens also exhibit injuries, which were probably sustained at or near the site. In addition, two of the seeps (AMNH locs. 3340 and 3386) contain an abundance of ammonite jaws as well as hooklike structures, both of which are attributed to *Hoploscaphites*, as described by Landman and Waage (1993). Because of the fragile

nature of these structures, their presence suggests that they did not experience much transport after the animals died. In addition, at AMNH loc. 3386, many of the body chambers are completely hollow or only partly filled with sediment, suggesting rapid burial without any strong currents on the sea floor. Thus, ammonites probably lived, died, and were buried at the seeps.

Another feature of the seeps that suggests that ammonites lived and died near or at the site is the preponderance of microconchs. At AMNH loc. 3386, which is represented by a large collection of *Hoploscaphites gilberti*, n. sp., from the limestone core of a seep, the measured set consists of 24 microconchs and 14 macroconchs. If incomplete specimens are included in the sample, the number of microconchs increases to 43 and the number of macroconchs increases to 27. Microconchs represent 61% of the total sample. At USGS Mesozoic loc. D3935, from the shale adjacent to several seeps, the measured set consists of 18 microconchs and 3 macroconchs. If incomplete specimens are included in the sample, the number of microconchs remains the same but the number of macroconchs increases to 4. Microconchs represent 82% of the total sample. According to most studies, macroconchs are interpreted as females, and microconchs as males (Makowski, 1962; Cobban, 1969). In analogy with many modern coleoids, males die soon after mating and their bodies settle to the sea floor (Boyle and Rodhouse, 2005). Thus, the overabundance of microconchs at these sites may indicate fatalities of males following mating. If so, these accumulations suggest that the ammonites died near or at the site.

Did the distribution of seeps in the Western Interior Seaway during the Late Cretaceous affect the biogeography of *Hoploscaphites gilberti*, n. sp.? In theory, individuals would have initially been distributed everywhere in the basin following hatching. As in other ammonites, the young post-embryonic animals were probably neutrally buoyant and, thus, would have lived in the water column rather than on the bottom (Landman et al., 1996). In analogy with modern cephalopods (Boyle and Rodhouse, 2005), they may have been active swimmers or passive vertical migrants drifting with surface currents for up to a period of several months. The ammonites may have preferred the seeps due to the local abundance of food and, presumably, would have remained there unless they were inadvertently transported away by currents. However, they could have lived in other parts of the basin if conditions were sufficiently hospitable.

The results of the present study suggest that *Hoploscaphites gilberti*, n. sp., occurs throughout the basin although it is more abundant at seeps such as that at AMNH loc. 3386 in the *Baculites scotti* Zone of the Pierre Shale, Butte County, South Dakota. However, it is also abundant in limestone and ironstone concretions in the shale surrounding seeps such as those at USGS Mesozoic loc. D1507 in the *B. scotti* Zone of the Pierre Shale on the west side of Baculite Mesa, Pueblo County, Colorado. This interval spans the Tepee Zone of Gilbert (1896), which, as the name implies, is characterized by numerous tepee buttes. The specimens of *H. gilberti*, n. sp., in this area were undoubtedly associated with the seeps, but it is difficult to establish which specimens lived at the same time with which seeps. *Hoploscaphites gilberti*, n. sp., is also present, although rarer, in concretions in shale in areas where seeps are absent, or at least not yet known, for example, in the *Didymoceras nebrascense* Zone of the Pierre Shale in Fall River County, South Dakota.

A comparison of specimens of *Hoploscaphites gilberti*, n. sp., in our collection suggests that specimens from seeps are smaller and more slender than those from nonseep sites. For exam-

ple, the average value of L_{MAX} of 3 macroconchs from nonseep sites (USNM 547296, 547304, and Sc 590A) is 68.3 mm. In contrast, the average value of L_{MAX} of 13 macroconchs from AMNH loc. 3386 is 39.9 mm. Many studies have suggested that the ontogenetic development of ammonites and cephalopods, in general, is very plastic and subject to environmental influence (Landman, 1988; Davis et al., 1996; Yacobucci, 2004). Thus, the difference in size between seep and nonseep specimens may reflect differences in the timing of maturation. Assuming that all specimens grew at approximately the same rate, the smaller size of the specimens at the seeps may imply that these individuals attained maturity at a younger age, possibly because of differences in the abundance of food between seep and nonseep sites.

In other biostratigraphic intervals, preliminary data also suggest that the same ammonite fauna is present at seep and at time-equivalent nonseep sites (Larson et al., 2013), although there is no indication of a size difference between adults of the same species. For example, in the *Didymoceras cheyennense* Zone in the Pierre Shale of South Dakota, the same species of *Baculites*, *Hoploscaphites*, *Didymoceras*, *Placenticerias*, and *Spiroxybeloceras* are present everywhere in the basin (Landman et al., 2012). Similarly, in the *Baculites compressus*-*B. cuneatus* Zones of the Pierre Shale of South Dakota, the same ammonite fauna is present at seep and nonseep sites (Landman et al., 2010; Larson et al., 2013). Indeed, ammonite-rich concretions from nonseep environments are especially abundant in this biostratigraphic interval and extend over an area of approximately 1000² km in southwestern South Dakota (Landman et al., 2010; Landman and Klofak, 2012).

TERMS, METHODS, AND REPOSITORIES

Most of the terms used to describe scaphites are reviewed by Landman et al. (2010). The adult shell consists of a closely coiled phragmocone and a slightly to strongly uncoiled body chamber (fig. 3). The adult phragmocone is the part of the phragmocone that is exposed in the adult shell, as compared to the part that is concealed inside. The point of exposure is the most adapical point of the adult phragmocone. The body chamber consists of the shaft, beginning near the last septum, and a hook terminating at the aperture. The point of recurvature is the point at which the hook curves backward.

Measurements of the adult shell are illustrated in figure 3. The maximum length of the adult shell (L_{MAX}) was measured from the venter of the adult phragmocone to the venter of the hook. The umbilical diameter of the adult shell (UD) was measured through the center of the umbilicus parallel to the line of maximum length. Whorl width (W) and whorl height (H) were measured at three points on the adult shell: (1) the phragmocone, along the line of maximum length (W_p , H_p), (2) the body chamber at midshaft (W_s , H_s), and (3) the hook at the point of recurvature (W_H , H_H). The width of the venter at midshaft (V_s) was measured between the ventrolateral margins on opposite sides of the venter. All measurements were made using electronic calipers on actual specimens, rather than on photos.

We calculated several ratios to describe the shape of the adult shell and facilitate comparisons among specimens. The ratios of whorl width to whorl height were calculated at three points on the shell (W_p/H_p , W_s/H_s , W_H/H_H), as described above, and provide a measure of the degree of whorl compression. The ratio of ventral width to whorl height at midshaft (V_s/H_s) provides an additional measure of the degree of whorl compression. The ratio of maximum length to whorl height on the

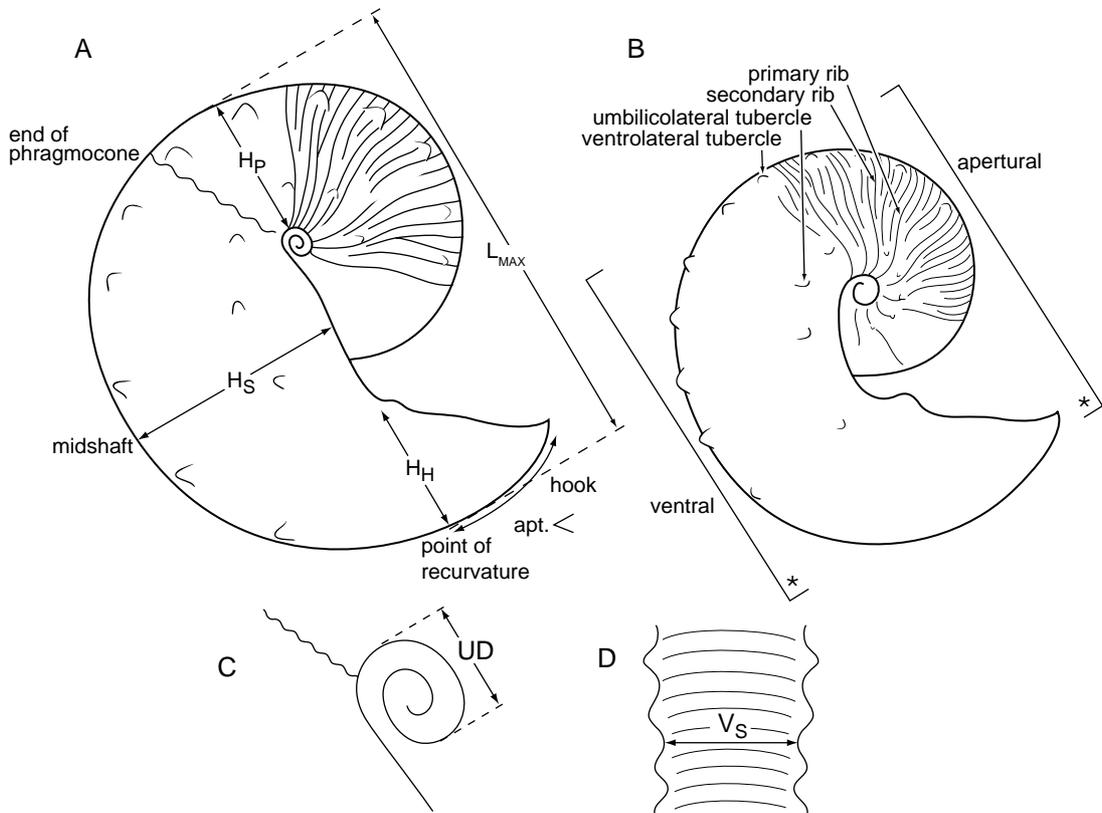


FIG. 3. Scaphite terminology. **A.** Macroconch, right lateral view. The shell is oriented in the probable floating position when the body was withdrawn into the body chamber. The umbilical seam of the shaft in macroconchs is straight with a slight umbilical bulge. Abbreviations: H_p = whorl height along the long axis; H_s = whorl height at midshaft; H_H = whorl height at the point of recurvature; L_{MAX} = maximum length along the long axis; apt. \angle = apertural angle. **B.** Microconch, right lateral view. In *Hoploscaphites gilberti*, n. sp., the microconch is approximately 80% of the size of the macroconch or, inversely, the macroconch is approximately 125% the size of the microconch. The umbilical seam of the shaft in microconchs is curved and follows the curvature of the venter. Specimens are photographed from lateral, ventral, and apertural views, as shown. Asterisks indicate the up position in each view. **C.** Close-up of the umbilicus of the macroconch showing the umbilical diameter measured parallel to the long axis (UD). **D.** View of the venter of the body chamber at midshaft, with the adoral direction toward the top, showing the width of the venter (V_s), as measured between the ventrolateral margins.

phragmocone along the line of maximum length (L_{MAX}/H_p) is a measure of the degree of uncoiling. The ratio of maximum length to whorl height at midshaft (L_{MAX}/H_s) is a measure of the degree of curvature of the body chamber in lateral view. If the outline of the body chamber in lateral view is a semicircle, the ratio of L_{MAX}/H_s equals 2. This ratio applies only to macroconchs because the umbilical seam of the body chamber usually coincides with the line of maximum length in these forms, and thus the whorl height is the distance from the line of maximum length to the venter of the body chamber (equivalent to the radius in the case of a semicircle).

The apertural angle is defined as by Landman and Waage (1993) and Machalski (2005). This angle is measured on photographs of specimens in lateral view. A line is drawn along the umbilical shoulder and another line is drawn along the apertural margin. The apertural angle

is the angle of intersection between these two lines, extending from approximately the point of recurvature to the aperture. We restricted this measurement to macroconchs, but even in these forms, it is sometimes difficult to know where to draw the line along the umbilical shoulder because it occasionally shows a bulge or sag.

A number of terms are used to describe ornamentation. Primary ribs originate near the umbilicus, whereas secondary ribs originate on the flanks or venter, either by branching or intercalation. The density of ribs is measured by counting the number of ribs/cm on the venter of the phragmocone along the line of maximum length, the midshaft, and the hook. In addition to ribs, the ornamentation includes tubercles, which are small conical swellings, and bullae, which are elongated in a radial direction (although it is sometimes difficult to distinguish them from raised ribs). Umbilicolateral bullae occur near the umbilicolateral margin and ventrolateral tubercles occur near the ventrolateral margin (fig. 3). We counted the number of bullae and tubercles on the phragmocone and body chamber of the adult shell. We recorded the distance between bullae and tubercles following the curvature of the shell on the umbilicolateral margin for umbilicolateral bullae, and on the ventrolateral margin for ventrolateral tubercles. The height of a tubercle is measured from its base to its tip, although this measurement is usually an underestimate due to imperfect preservation. We also recorded the number of ribs that join a bulla (or tubercle) dorsally, the number of ribs that branch from it ventrally, and the number of ribs that intercalate between consecutive bullae (or tubercles).

The repository of specimens described in the text is indicated by a prefix, as follows: Division of Paleontology (Invertebrates), American Museum of Natural History (AMNH), New York, New York; Steven D. Jorgensen Collection (Sc), Highlands Ranch, Colorado; and U.S. National Museum (USNM), Washington, D.C. The localities of the specimens are shown in figure 1 and are listed in the appendix.

SYSTEMATIC PALEONTOLOGY

CLASS CEPHALOPODA CUVIER, 1797

ORDER AMMONOIDEA ZITTEL, 1884

SUBORDER ANCYLOCERATINA WIEDMANN, 1966

SUPERFAMILY SCAPHITOIDEA GILL, 1871

FAMILY SCAPHITIDAE GILL, 1871

SUBFAMILY SCAPHITINAE GILL, 1871

Genus *Hoploscaphites* Nowak, 1911

(= *Jeletzkytes* Riccardi, 1983: 14)

TYPE SPECIES: *Ammonites constrictus* J. Sowerby, 1817: 189, pl. A, fig. 1, by original designation.

DIAGNOSIS: "Small to large scaphites, strongly dimorphic, with broad variation in degree of whorl compression ranging from slender to robust, with involute phragmocone, short to long shaft, and weakly recurved hook; apertural angle ranging from approximately 35° to 85°; aperture constricted with dorsal projection; ribs straight to flexuous, increasing by branching

and intercalation, with weak to strong adoral projection on venter; adult shell with or without umbilicolateral, flank, and ventrolateral tubercles; suture fairly indented, with symmetric to slightly asymmetric bifid first lateral lobe” (Landman et al., 2010).

DISCUSSION: Scaphitid ammonites of the genus *Hoploscaphites* first appear in the Western Interior of North America in the lower Campanian and persist until the upper Maastrichtian (Larson et al., 1997). Approximately 10 species have been described so far (Meek, 1876; Coryell and Salmon, 1934; Cobban and Jeletzky, 1965; Riccardi, 1983; Landman and Waage, 1993; Landman et al., 2010), and at least a half dozen are yet to be described. Several of these species were previously attributed to *Jeletzkytes*, but this genus was synonymized with *Hoploscaphites* because the two genera share the same shell shape, pattern of ornamentation, and suture, and only differ in the degree of whorl compression and, as a consequence, the flexuosity of the ribs and size of the tubercles (Wright, 1996; Landman et al., 2010). Nearly all of the species in the Western Interior of North America are endemic to this basin but their phylogeny has not yet been worked out. These species are closely related to other species in Greenland and northwest Europe, and it is difficult to characterize the evolution of the North American species without reference to species in other areas. Such studies will help shed light on the biogeography of *Hoploscaphites* and the timing and extent of the connections between the Western Interior of North America and northwest Europe.

Hoploscaphites gilberti, n. sp.

Figures 4–13

Scaphites nodosus. Gilbert, 1896: pl. 63, fig. 3.

Hoploscaphites gilli. Cobban and Jeletzky, 1965: pl. 95, fig. 1A–D.

DIAGNOSIS: Adult shell compressed, with rounded to elongate outline in lateral view; strongly dimorphic; macroconchs with relatively short shaft and recurved hook leaving almost no gap between exposed phragmocone and hook; apertural angle averages 50°; umbilical seam straight in lateral view; microconchs with longer shaft and more recurved hook leaving larger gap between exposed phragmocone and hook; umbilical seam concave in lateral view; in both dimorphs, intercostal whorl section of shaft subquadrate with fairly flat, subparallel flanks and broadly rounded venter; ribs slightly flexuous with weak adoral projection on venter; umbilicolateral bullae or raised ribs on body chamber; ventrolateral tubercles on exposed phragmocone and body chamber, usually extending to aperture; suture simple with broad, asymmetrically bifid first lateral saddle and narrow, symmetrically to asymmetrically bifid first lateral lobe.

ETYMOLOGY: For Grove Karl Gilbert, who first illustrated this species in 1896 in his seminal study in which he first described the tepee buttes of the Pierre Shale of Colorado.

TYPES: Holotype is AMNH 64559, a macroconch, from the *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. Paratypes are USNM 547296, a macroconch, from the *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3464, Pueblo County, Colorado; USNM 547293, a macroconch, from the *Baculites scotti* Zone, USGS Mesozoic loc. D84, Pueblo County, Colorado; USNM 28362, a microconch, from the Pierre Shale, USGS loc. 1359, Pueblo County, Colorado, as illustrated by Gilbert (1896: pl. 63, fig. 3); AMNH 64573, a

TABLE 2

Measurements of *Hoploscaphites gilberti*, n. sp., macroconchs

See figure 3 for description of measurements. All measurements are in mm except for apertural angle, which is in degrees. * = Pierre Shale, Fall River County, South Dakota.

Specimen Number	Locality	Zone	L _{MAX}	L _{MAX} / H _P	L _{MAX} / H _S	Apt <	UD	UD/ L _{MAX}	W _P / H _P	W _S / H _S	W _H / H _H	V _S / H _S
AMNH 64531	AMNH 3386	<i>B. scotti</i>	—	—	—	73.0	—	—	—	0.86	1.07	0.58
AMNH 64559	AMNH 3386	<i>B. scotti</i>	32.0	3.23	2.34	42.5	3.38	0.11	0.92	0.83	1.02	0.65
AMNH 64561	AMNH 3386	<i>B. scotti</i>	35.2	3.09	2.11	—	2.02	0.06	0.87	0.78	0.96	—
AMNH 64587	AMNH 3386	<i>B. scotti</i>	32.6	3.26	2.28	51.5	3.46	0.11	0.90	0.76	1.07	0.60
AMNH 64601	AMNH 3386	<i>B. scotti</i>	40.5	3.21	2.45	47.5	3.95	0.10	0.87	0.82	1.01	—
AMNH 64646	AMNH 3386	<i>B. scotti</i>	37.0	3.27	—	—	3.58	0.10	0.92	—	0.97	—
AMNH 64699	AMNH 3386	<i>B. scotti</i>	55.2	3.27	2.05	71.5	5.61	0.10	1.09	0.90	—	0.59
AMNH 81100	AMNH 3386	<i>B. scotti</i>	41.8	3.40	2.34	45.0	3.79	0.09	1.02	0.80	1.06	0.64
AMNH 81104	AMNH 3386	<i>B. scotti</i>	46.7	3.22	2.07	—	4.72	0.10	0.96	—	—	—
AMNH 81117	AMNH 3340	<i>D. nebrascense</i>	53.7	2.97	—	55.0	3.90	0.07	0.81	—	1.01	—
AMNH 81443	AMNH 3386	<i>B. scotti</i>	37.7	3.06	—	—	3.61	0.10	0.89	—	1.04	—
AMNH 81469	AMNH 3386	<i>B. scotti</i>	45.2	—	—	—	—	—	—	—	—	—
AMNH 81473	AMNH 3386	<i>B. scotti</i>	37.2	3.35	2.42	—	5.08	0.14	0.90	—	1.05	—
AMNH 81478	AMNH 3386	<i>B. scotti</i>	32.1	3.00	—	—	3.40	0.10	0.92	—	1.11	—
AMNH 83717	AMNH 3386	<i>B. scotti</i>	45.0	3.04	2.07	74.0	—	—	0.89	0.74	1.03	0.53
Sc 590A	*	<i>D. nebrascense</i>	57.7	3.04	2.29	67.0	4.03	0.07	0.99	0.90	0.98	0.66
Sc 1001B	AMNH 3340	<i>D. nebrascense</i>	35.9	3.02	2.18	41.0	4.10	0.11	—	—	—	0.59
USNM 547293	USGS D84	<i>B. scotti</i>	37.6	—	—	37.5	3.12	0.08	—	—	0.80	—
USNM 547294	USGS D84	<i>B. scotti</i>	54.4	—	2.06	62.5	—	—	—	—	—	—
USNM 547295	USGS D3941	<i>B. scotti</i>	45.4	3.07	—	64.0	4.01	0.09	0.81	—	—	—
USNM 547296	USGS D3464	<i>B. scotti</i>	67.3	3.24	2.21	37.0	5.00	0.07	0.99	1.03	1.24	0.78

Specimen Number	Locality	Zone	L_{MAX}	L_{MAX}/H_P	L_{MAX}/H_S	Apt <	UD	UD/ L_{MAX}	W_P/H_P	W_S/H_S	W_H/H_H	V_S/H_S
USNM 547297	USGS 750	–	40.6	–	–	–	2.47	0.06	–	0.70	0.87	0.57
USNM 547298	?	<i>B. scotti</i>	34.1	3.16	2.30	43.0	3.12	0.09	0.79	0.80	0.94	–
USNM 547299	USGS D3935	<i>B. scotti</i>	32.6	–	2.09	–	2.65	0.08	–	0.76	–	0.66
USNM 547300	USGS D1803	<i>D. nebrascense</i>	35.2	2.91	2.27	–	–	–	–	0.70	0.92	–
USNM 547301	USGS D8550	<i>B. scotti</i>	36.1	3.14	2.01	46.5	3.51	0.10	0.87	0.63	0.86	–
USNM 547302	USGS D1509	<i>B. scotti</i>	44.6	3.19	2.30	54.0	3.85	0.09	0.89	0.88	0.91	0.65
USNM 547303	USGS D3935	<i>B. scotti</i>	27.9	2.97	2.21	37.5	2.52	0.09	0.82	0.77	0.99	0.55
USNM 547304	USGS D379	<i>B. scotti</i>	79.8	3.05	2.26	40.5	6.05	0.08	–	0.95	1.15	0.75
USNM 547305	USGS D3935	<i>B. scotti</i>	40.8	–	–	–	–	–	–	–	–	–
USNM 547339	USGS D84	<i>B. scotti</i>	37.8	–	–	–	–	–	–	–	–	–
USNM 547349	USGS D2621	<i>B. scotti</i>	44.6	3.00	–	–	3.72	0.08	–	–	–	–

microconch, from the *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota; and AMNH 81467, a microconch, from the *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota.

MATERIAL: Approximately 150 specimens of which 33 macroconchs and 70 microconchs comprise the measured set (tables 2 and 3). All of the specimens are from the *Baculites scotti* and overlying *Didymoceras nebrascense* zones of the Pierre Shale in South Dakota, Colorado, Montana, and Wyoming. All of the specimens are internal molds without any shell material.

MACROCONCH DESCRIPTION: In the measured sample, L_{MAX} averages 42.7 mm and ranges from 27.9 to 79.8 mm (fig. 4, table 2). The ratio of the size of the largest specimen to that of the smallest is 2.86. The distribution is unimodal with a peak at 35–40 mm. However, in samples from single localities, the size range is much more restricted (fig. 5). At USGS Mesozoic loc. D3935, L_{MAX} ranges from 35.2 to 40.4 mm and the ratio of the size of the largest specimen to that of the smallest is 1.15. At AMNH loc. 3386, L_{MAX} ranges from 32.0 to 55.2 mm and the ratio of the size of the largest specimen to that of the smallest is 1.72.

Adults are slender, with a rounded to elongate outline in lateral view. For example, the outline is rounded in USNM 547292 ($L_{MAX}/H_S = 2.00$), whereas it is elongate in AMNH 64601 ($L_{MAX}/H_S = 2.45$). The exposed phragmocone occupies approximately one-half whorl. It terminates slightly below the line of maximum length. The umbilicus is small and deep, averaging 3.79 mm in diameter. The ratio of UD/ L_{MAX} averages 0.09.

The body chamber consists of a short shaft and recurved hook, extending slightly beyond the coiled portion, leaving a small gap. L_{MAX}/H_P averages 3.13 and ranges from 2.91 to 3.27

TABLE 3
Measurements of *Hoploscaphites gilberti*, n. sp., microconchs
 See figure 3 for description of measurements. All measurements are in mm.

Specimen Number	Locality	Zone	L _{MAX}	L _{MAX} /H _P	UD	UD/L _{MAX}	W _P /H _P	W _S /H _S	W _H /H _H	V _S /H _S
AMNH 63525	AMNH 3386	<i>B. scotti</i>	37.1	3.34	3.96	0.11	—	0.78	1.02	—
AMNH 63528	AMNH 3386	<i>B. scotti</i>	33.3	3.74	3.47	0.10	1.10	0.88	1.08	—
AMNH 63529	AMNH 3386	<i>B. scotti</i>	31.8	3.42	3.27	0.10	0.85	—	—	—
AMNH 63532	AMNH 3386	<i>B. scotti</i>	—	—	4.02	—	—	—	0.97	—
AMNH 63534	AMNH 3386	<i>B. scotti</i>	32.0	3.11	4.06	0.13	1.02	0.92	—	0.71
AMNH 63535	AMNH 3386	<i>B. scotti</i>	26.8	—	—	—	—	0.94	—	0.68
AMNH 63536	AMNH 3494	<i>D. nebrascense</i>	36.1	3.57	4.14	0.11	0.96	1.02	—	0.66
AMNH 63538	AMNH 3494	<i>D. nebrascense</i>	38.3	3.58	4.70	0.12	1.07	1.01	1.08	—
AMNH 64493	AMNH 3386	<i>B. scotti</i>	39.8	—	—	—	—	—	—	—
AMNH 64549	AMNH 3386	<i>B. scotti</i>	36.0	3.75	3.81	0.10	0.93	—	1.06	—
AMNH 64573	AMNH 3386	<i>B. scotti</i>	34.7	3.44	4.28	0.12	0.88	1.01	1.04	0.73
AMNH 64575	AMNH 3386	<i>B. scotti</i>	30.4	3.01	2.91	0.10	—	0.96	0.97	0.74
AMNH 64589	AMNH 3386	<i>B. scotti</i>	35.8	3.44	—	—	0.90	0.76	1.04	0.55
AMNH 64603	AMNH 3386	<i>B. scotti</i>	34.1	3.48	4.10	0.12	0.87	0.93	1.04	—
AMNH 64615	AMNH 3386	<i>B. scotti</i>	38.0	3.36	4.37	0.12	0.88	0.93	1.08	0.70
AMNH 64617	AMNH 3386	<i>B. scotti</i>	—	—	2.29	—	1.03	—	—	—
AMNH 64618	AMNH 3340	<i>D. nebrascense</i>	39.1	—	4.65	0.12	—	—	—	—
AMNH 64631	AMNH 3386	<i>B. scotti</i>	34.2	3.26	3.55	0.10	0.93	0.90	0.96	0.61
AMNH 64645	AMNH 3386	<i>B. scotti</i>	—	—	2.30	—	—	0.98	1.06	0.71
AMNH 64659	AMNH 3386	<i>B. scotti</i>	35.5	3.48	3.88	0.11	1.00	0.95	0.99	0.68
AMNH 64660	AMNH 3386	<i>B. scotti</i>	27.6	3.33	3.47	0.13	0.87	—	—	—
AMNH 64677	AMNH 3386	<i>B. scotti</i>	34.7	3.07	4.23	0.12	0.88	0.89	—	—
AMNH 81094	AMNH 3340	<i>D. nebrascense</i>	36.3	—	3.56	0.10	—	—	—	—
AMNH 81098	AMNH 3386	<i>B. scotti</i>	37.4	3.14	—	—	0.81	—	—	—
AMNH 81108	AMNH 3386	<i>B. scotti</i>	28.8	3.35	4.19	0.15	0.86	—	—	—
AMNH 81118	AMNH 3340	<i>D. nebrascense</i>	44.1	3.34	4.32	0.10	0.90	0.88	—	—
AMNH 81467	AMNH 3386	<i>B. scotti</i>	35.3	3.57	3.49	0.10	0.92	0.97	1.10	—
AMNH 81451	AMNH 3386	<i>B. scotti</i>	34.3	3.59	—	—	1.01	0.91	—	—
AMNH 81472	AMNH 3386	<i>B. scotti</i>	26.4	3.18	2.52	0.10	0.80	0.83	1.08	0.71
AMNH 81503	AMNH 3344	<i>D. nebrascense</i>	33.3	3.33	3.61	0.11	—	0.81	0.99	—
Sc 1001J	AMNH 3340	<i>D. nebrascense</i>	37.6	—	3.64	0.10	—	0.89	—	—
Sc 1289A	AMNH 3340	<i>D. nebrascense</i>	40.0	3.74	4.14	0.10	0.93	0.84	1.05	0.57
USNM 28362	USGS 1359	<i>B. scotti</i>	34.0	3.24	2.56	0.08	0.87	0.93	1.07	0.75
USNM 547306	USGS D3935	<i>B. scotti</i>	28.1	3.16	3.01	0.11	0.82	0.98	—	—
USNM 547307	USGS D3935	<i>B. scotti</i>	23.8	3.35	3.07	0.13	0.89	0.89	0.94	0.75
USNM 547308	USGS D3935	<i>B. scotti</i>	36.0	3.43	—	—	0.90	0.81	0.88	—

Specimen Number	Locality	Zone	L _{MAX}	L _{MAX} /H _P	UD	UD/L _{MAX}	W _P /H _P	W _S /H _S	W _H /H _H	V _S /H _S
USNM 547309	USGS D3935	<i>B. scotti</i>	27.2	3.20	–	–	0.78	0.86	0.82	0.69
USNM 547310	USGS D3935	<i>B. scotti</i>	26.2	3.54	–	–	0.85	0.84	1.04	0.80
USNM 547311	USGS D3935	<i>B. scotti</i>	30.6	3.26	–	–	–	0.88	1.02	0.67
USNM 547312	USGS D3935	<i>B. scotti</i>	25.8	2.93	–	–	–	0.97	1.02	–
USNM 547313	USGS D3935	<i>B. scotti</i>	31.5	2.89	3.99	0.13	0.82	0.90	–	–
USNM 547314	USGS D3935	<i>B. scotti</i>	27.3	2.90	3.15	0.12	–	–	0.93	–
USNM 547315	USGS D3935	<i>B. scotti</i>	26.8	3.35	3.23	0.12	0.89	0.89	1.04	–
USNM 547316	USGS D3935	<i>B. scotti</i>	25.5	3.49	3.25	0.13	–	0.89	–	–
USNM 547317	USGS D3936	<i>B. scotti</i>	25.7	3.21	2.66	0.10	0.85	0.86	1.11	–
USNM 547318	USGS D3935	<i>B. scotti</i>	27.0	3.00	–	–	–	–	1.08	–
USNM 547319	USGS D3935	<i>B. scotti</i>	23.9	3.41	3.13	0.13	0.83	–	–	–
USNM 547320	USGS D3935	<i>B. scotti</i>	31.0	3.48	–	–	0.94	0.88	1.06	–
USNM 547321	USGS D3935	<i>B. scotti</i>	29.4	3.20	2.77	0.09	0.85	0.79	0.93	0.62
USNM 547322	USGS D8550	<i>B. scotti</i>	29.1	3.34	3.99	0.14	0.83	0.85	0.99	0.68
USNM 547323	USGS 750	?	34.5	–	–	–	–	–	1.09	0.73
USNM 547324	USGS D8721	<i>B. scotti</i>	39.1	3.20	4.10	0.10	0.82	0.88	1.09	0.66
USNM 547325	USGS D3935	<i>B. scotti</i>	32.6	3.29	3.35	0.10	0.88	0.88	1.00	0.61
USNM 547326	USGS D3935	<i>B. scotti</i>	24.2	3.51	2.46	0.10	0.83	0.88	1.01	0.71
USNM 547327	USGS D3936	<i>B. scotti</i>	34.5	3.45	3.54	0.10	0.86	0.92	0.99	0.69
USNM 547330	USGS D1509	?	28.2	–	3.26	0.12	–	0.96	1.08	0.69
USNM 547331	USGS D3935	<i>B. scotti</i>	27.2	3.40	2.76	0.10	–	0.82	–	0.64
USNM 547332	USGS D3935	<i>B. scotti</i>	26.8	–	–	–	–	0.81	1.05	0.65
USNM 547335	USGS D285	<i>B. scotti</i>	40.8	3.40	4.59	0.11	–	0.78	–	0.56
USNM 547336	USGS D2621	<i>B. scotti</i>	34.8	–	–	–	–	1.06	–	0.76
USNM 547337	USGS D379	<i>B. scotti</i>	41.4	–	–	–	–	–	1.06	0.64
USNM 547338	USGS D84	<i>B. scotti</i>	37.1	3.04	–	–	0.96	1.01	1.04	0.78
USNM 547340	USGS D2629	<i>D. nebrascense</i>	43.7	3.44	3.09	0.07	0.85	–	0.95	0.53
USNM 547341	USGS 1362	<i>B. scotti</i>	35.2	3.26	4.11	0.12	0.87	0.91	1.06	0.65
USNM 547342	USGS D3935	<i>B. scotti</i>	26.8	3.39	3.80	0.14	0.85	0.98	1.05	0.83
USNM 547344	USGS 1362	<i>B. scotti</i>	26.7	3.47	2.90	0.11	0.87	–	1.10	0.64
USNM 547345	USGS D3935	<i>B. scotti</i>	35.4	3.31	4.40	0.12	0.88	0.88	0.90	0.67
USNM 547346	USGS D84	<i>B. scotti</i>	34.8	–	3.76	0.11	0.89	–	–	–
USNM 547347	USGS ≈D1509	<i>B. scotti</i>	33.0	–	–	–	–	–	–	–
USNM 547350	USGS D2792	<i>B. scotti</i>	40.4	–	–	–	–	0.93	–	0.65
USNM 547603	USGS D8551	<i>B. scotti</i>	42.0	3.56	5.26	0.13	1.14	0.99	–	0.75

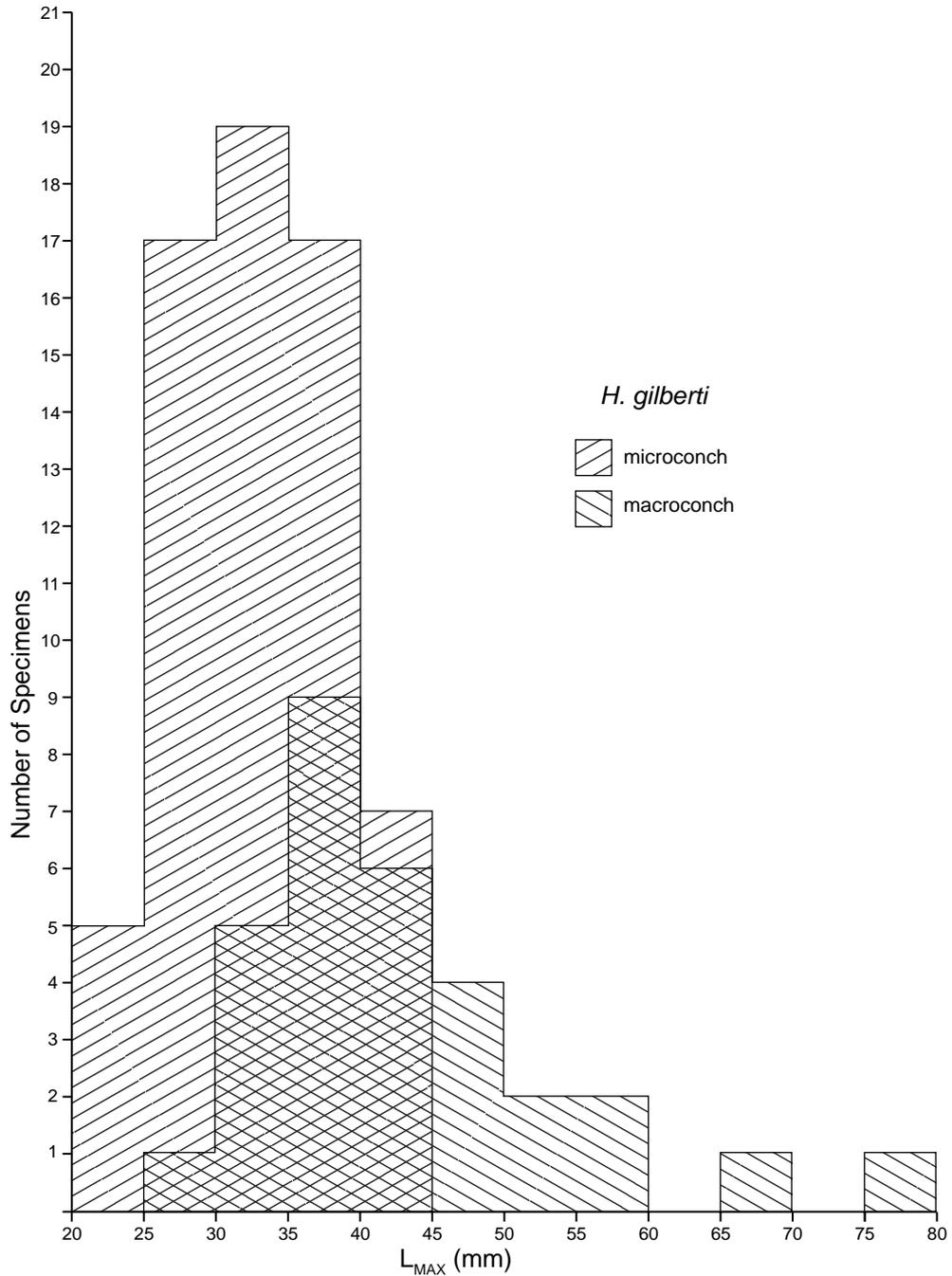


FIG. 4. Size-frequency histogram of *Hoploscaphites gilberti*, n. sp., Pierre Shale, *Baculites scotti*-*Didymoceras nebrascense* zones, based on the samples in tables 1 and 2.

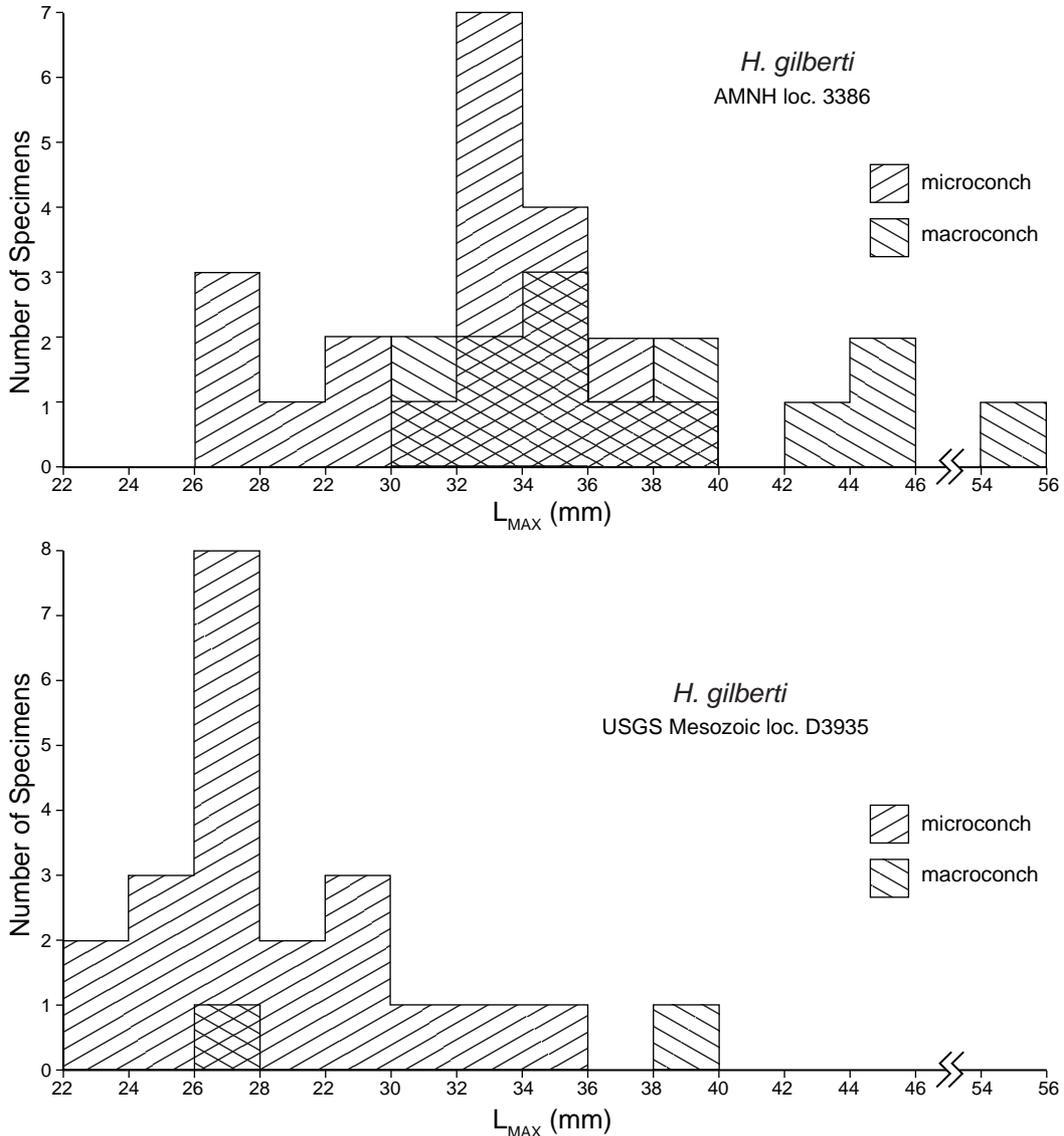
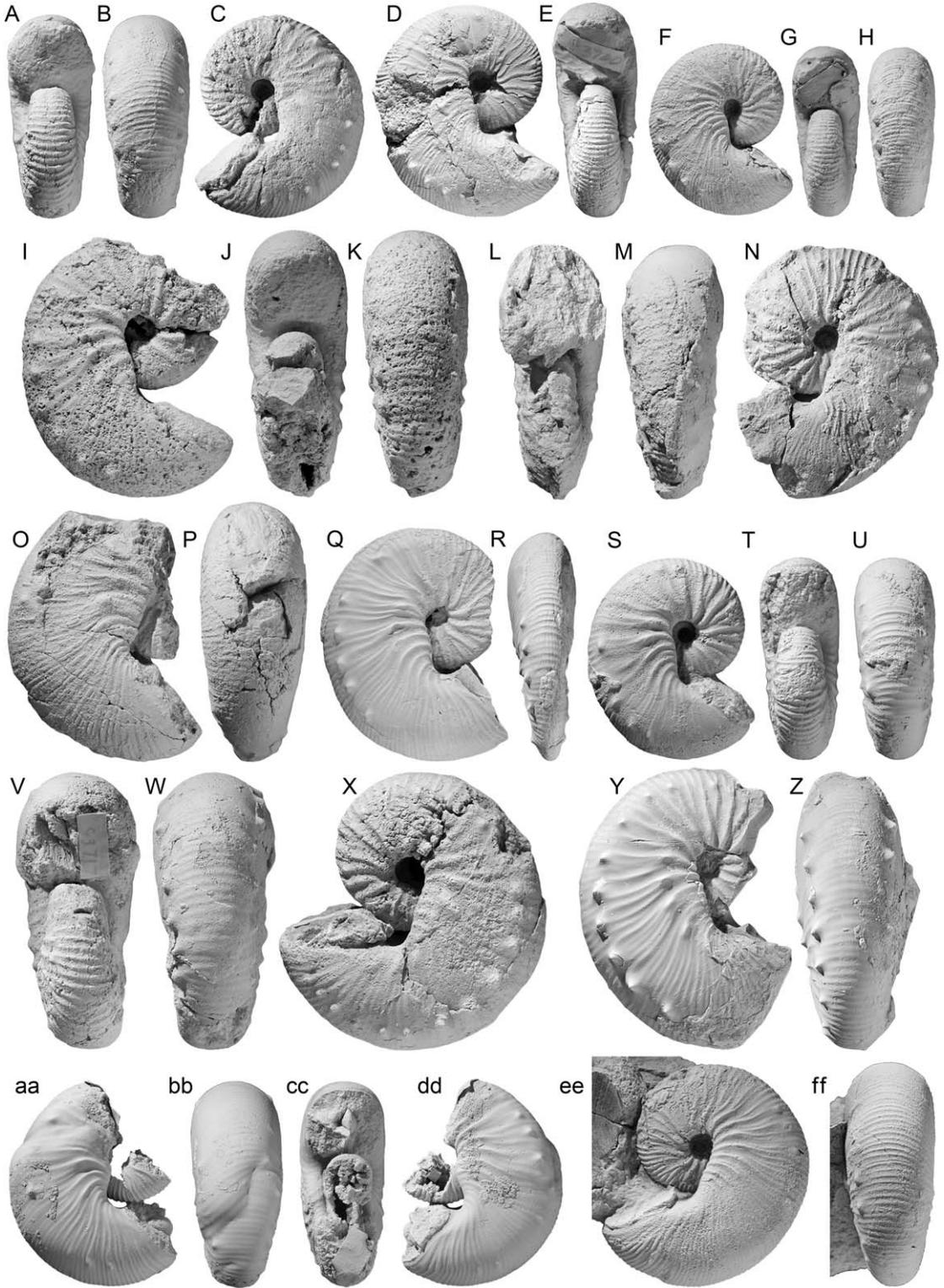


FIG. 5. Size-frequency histogram of *Hoploscaphites gilberti*, n. sp., at two localities in the *Baculites scotti* Zone, Pierre Shale, South Dakota and Colorado: AMNH loc. 3386 (top); USGS Mesozoic loc. D3935 (bottom).

(3.23 in the holotype). The hook is weakly reflected, as indicated by a low apertural angle, averaging 52.1° and ranging from 32.5 to 74.0° . The apertural lip is flexuous with a deep constriction. In lateral view, the umbilical shoulder of the shaft is convex or straight, depending on the presence or absence of an umbilical swelling. The umbilical swelling appears as an elongate bulge that extends several millimeters along the shaft, as in USNM 547301 (fig. 7I–K).

The whorl section of the phragmocone along the line of maximum length is compressed. W_p/H_p averages 0.91 and ranges from 0.79 to 1.09 (0.92 in the holotype). The intercostal whorl section is subquadrate with maximum width at one-third whorl height. The umbilical wall is



steep and subvertical and the umbilical shoulder is sharply rounded. The flanks are very broadly rounded to flat, converging toward the venter. The ventrolateral shoulder is sharply rounded and the venter is more broadly rounded.

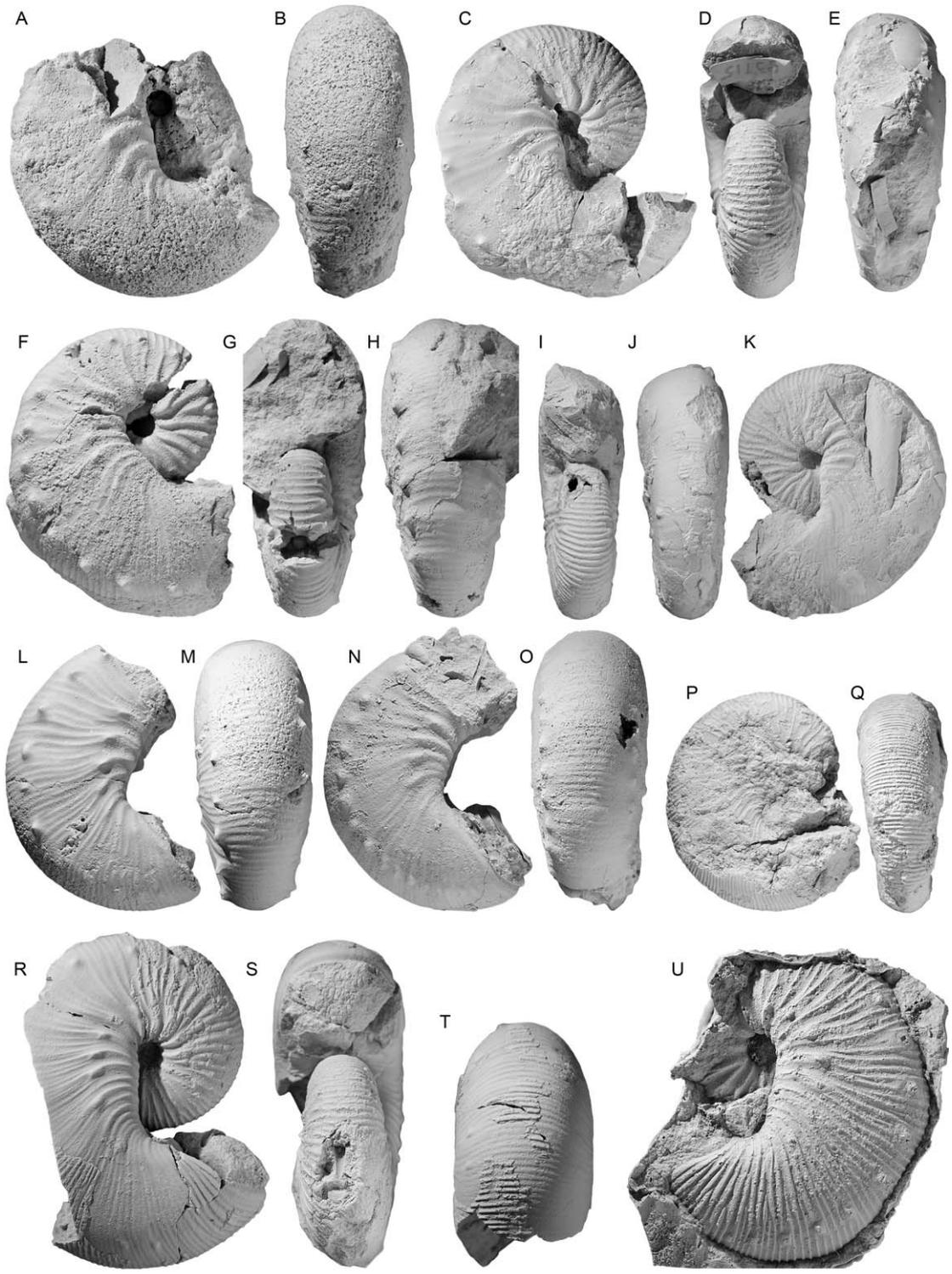
Whorl width gradually increases as the shell passes into the shaft, and reaches its maximum value at the point of recurvature. Whorl height increases more abruptly and reaches its maximum value at midshaft, after which it decreases slightly. The whorl section at midshaft is slightly more compressed than that of the phragmocone along the line of maximum length. W_S/H_S averages 0.81 and ranges from 0.70 to 1.03 (0.83 in the holotype). The ratio of V_S/H_S averages 0.63 and ranges from 0.53 to 0.78 (0.65 in the holotype). The intercostal whorl section at midshaft is subquadrate. The umbilical shoulder is sharply rounded on the shaft, becoming more broadly rounded on the hook. The flanks are subparallel and very broadly rounded to nearly flat, with maximum width at one-third whorl height. In some specimens such as USNM 547294 (fig. 8F), the inner flanks are broadly rounded, and the outer flanks are flattened and converge toward the venter. The ventrolateral shoulder is sharply rounded and the venter is more broadly rounded.

The whorl section becomes less compressed from midshaft to the point of recurvature. W_H/H_H averages 1.00 and ranges from 0.86 to 1.24 (1.02 in the holotype). The intercostal whorl section also becomes slightly more ovoid, with maximum width at one-half whorl height.

All specimens, regardless of their size, display the same pattern of ornamentation consisting of fine, flexuous ribs, umbilicolateral bullae, and ventrolateral tubercles, which usually extend to the aperture. Although this pattern of ornamentation is the same among all specimens, the spacing of the ribs and the size of the umbilicolateral bullae and ventrolateral tubercles vary depending on adult size.

Starting at the point of exposure, primary ribs arise at the umbilical seam and strengthen across the umbilical wall and shoulder. They are rectiradiate to prorsiradiate on the flanks. They are straight or weakly flexuous, bending slightly backward on the inner flanks, slightly forward on the midflanks, and slightly backward again on the outer flanks. They are sharp, narrow, and

FIG. 6. *Hoploscaphites gilberti*, n. sp., macroconchs. **A–C**. AMNH 64587, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **A**, Apertural; **B**, ventral; **C**, left lateral. **D, E**. USNM 547298, *Baculites scotti* Zone, locality unknown, but probably El Paso County, Colorado. **D**, Right lateral; **E**, apertural. **F–H**. USNM 547303, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935. Pueblo County, Colorado. **F**, Right lateral; **G**, apertural; **H**, ventral. **I–K**. AMNH 81100, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **I**, Right lateral; **J**, apertural; **K**, ventral. **L–N**. AMNH 64601, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **L**, Apertural; **M**, ventral; **N**, left lateral. **O, P**. AMNH 64550, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. **O**, Right lateral; **P**, ventral. **Q, R**. USNM 547293, paratype, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D84, Pueblo County, Colorado. **Q**, Right lateral; **R**, ventral. **S–U**. AMNH 64559, holotype, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **S**, Right lateral; **T**, apertural; **U**, ventral. **V–X**. AMNH 83717, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **V**, Apertural; **W**, ventral; **X**, left lateral. **Y, Z**. USNM 547302, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D1509, Pueblo County, Colorado. **Y**, Right lateral; **Z**, ventral. **aa–dd**. AMNH 64562, with injury on body chamber, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. **aa**, Right lateral; **bb**, ventral; **cc**, apertural; **dd**, left lateral. **ee, ff**. Sc 1001B, *Didymoceras nebrascense* Zone, AMNH loc. 3340, Fall River County, South Dakota. **ee**, Left lateral; **ff**, ventral. Specimens $\times 1$.



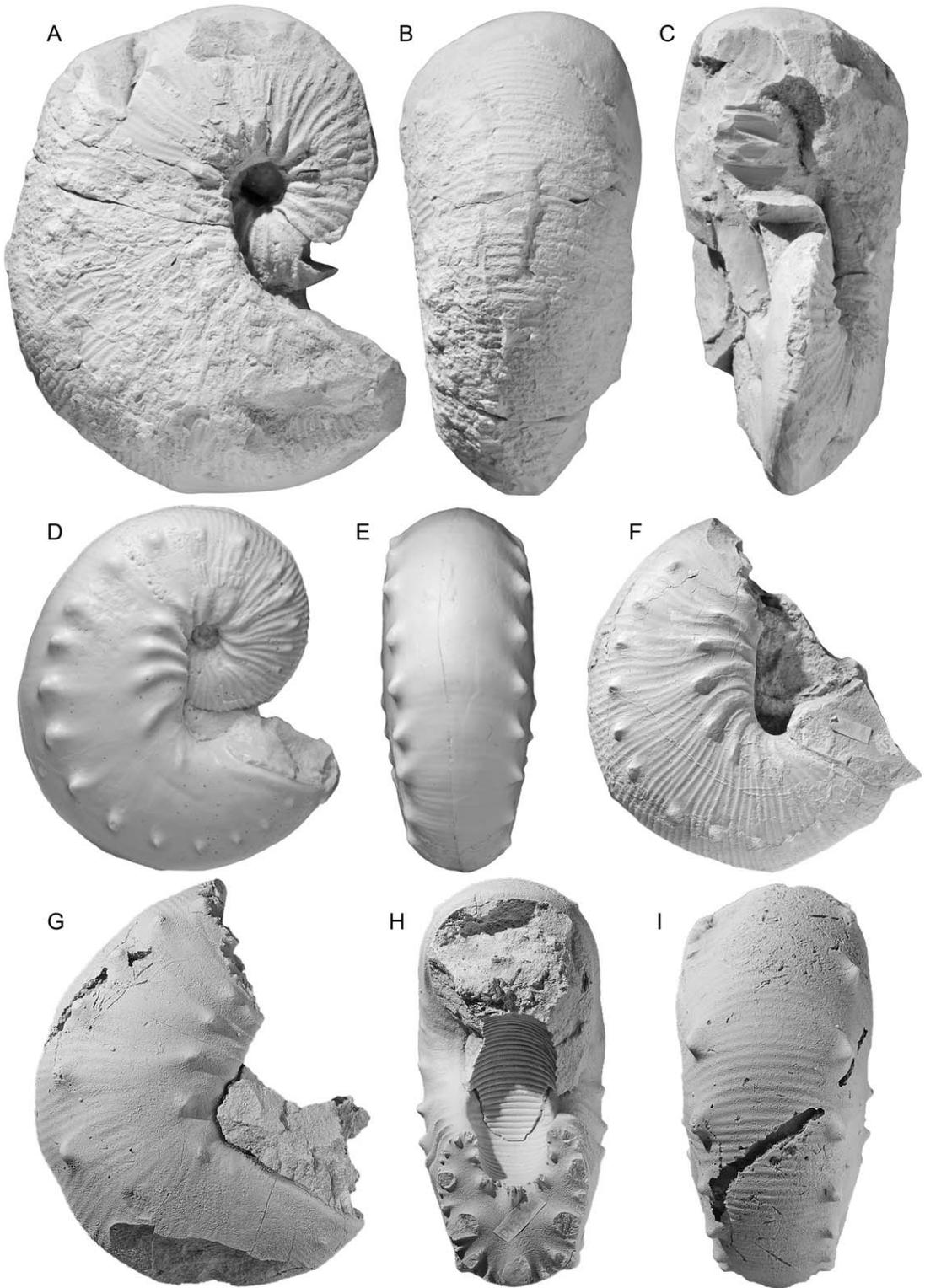
equally strong on the venter, which they cross with a slight adoral projection. The rib density on the phragmocone along the line of maximum length ranges from 7 to 14 ribs/cm (11 ribs/cm on the holotype). Branching and intercalation occur at one-third and two-thirds whorl height, at the umbilicolateral and ventrolateral margin, respectively.

On the body chamber, ribs arise at the umbilical seam and are rursiradiate on the umbilical wall and shoulder, becoming more rectiradiate toward the adoral end of the shaft. In larger, more coarsely ornamented specimens, such as USNM 547304 (fig. 8A–C), the ribs on the umbilical wall and shoulder are raised into barlike bullae. Ribs weaken on the flanks; they are rectiradiate to slightly rursiradiate on the adapical portion of the shaft, becoming more prorsiradiate on the adoral portion of the shaft. Ribs are narrow and slightly flexuous, swinging gently backward on the inner flanks, more strongly forward on the midflanks, and weakly backward again on the outer flanks. This flexuosity diminishes on the hook. Branching and intercalation occur at one-third and two-thirds whorl height, at the umbilicolateral and ventrolateral margin, respectively. Ribs cross the venter with a marked forward projection. The rib density at midshaft ranges from 8 to 13 ribs/cm (10 ribs/cm on the holotype). The rib density remains the same or increases on the hook (17 ribs/cm on the holotype).

In most small specimens, such as the holotype, umbilicolateral bullae are absent on the phragmocone. Instead, the primary ribs in this area are strong and adorally concave. In larger specimens, umbilicolateral bullae appear midway or near the adoral end of the exposed phragmocone. For example, four umbilicolateral bullae are present on the adoral portion of the exposed phragmocone in USNM 547296 (fig. 9A–C). Bullae are relatively evenly spaced, with a maximum distance between consecutive bullae of 5 mm. As many as two ribs intercalate between bullae; one rib joins a bulla dorsally and two or three ribs branch from it ventrally.

Umbilicolateral bullae are usually, but not invariably, present on the body chamber. If bullae are absent, as in the holotype, the primary ribs in this area are strong and adorally concave. If bullae are present, they occur on the primary ribs at one-third whorl height. In some specimens, such as USNM 547302, the bullae are elevated into tubercles 1.5 mm high (fig. 6Y, Z). The maximum total number of umbilicolateral bullae on the body chamber is 8 (USNM 547294), and the maximum total number on the entire shell is 13 (USNM 547304). The bullae are more or less evenly spaced on the adapical part of the shaft, becoming slightly more widely

FIG. 7. *Hoploscaphites gilberti*, n. sp., macroconchs. **A, B.** AMNH 63527, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. A, Right lateral; B, ventral. **C–E.** USNM 547295, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3941, Pueblo County, Colorado. C, Right lateral; D, apertural; E, ventral. **F–H.** AMNH 81104, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. F, Right lateral; G, apertural; H, ventral. **I–K.** USNM 547301, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D8550, El Paso County, Colorado. I, Apertural; J, ventral; K, left lateral. **L, M.** AMNH 64531, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. L, Right lateral, M, ventral. **N, O.** AMNH 81102, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. N, Right lateral; O, ventral. **P, Q.** USNM 547300, *Didymoceras nebrascense* Zone, Pierre Shale, USGS Mesozoic loc. D1803, Pueblo County, Colorado. P, Right lateral; Q, ventral. **R–T.** AMNH 81117, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. R, Right lateral; S, apertural; T, anterior ventral. **U.** AMNH 64408, rubber peel, left lateral, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. Specimens $\times 1$.



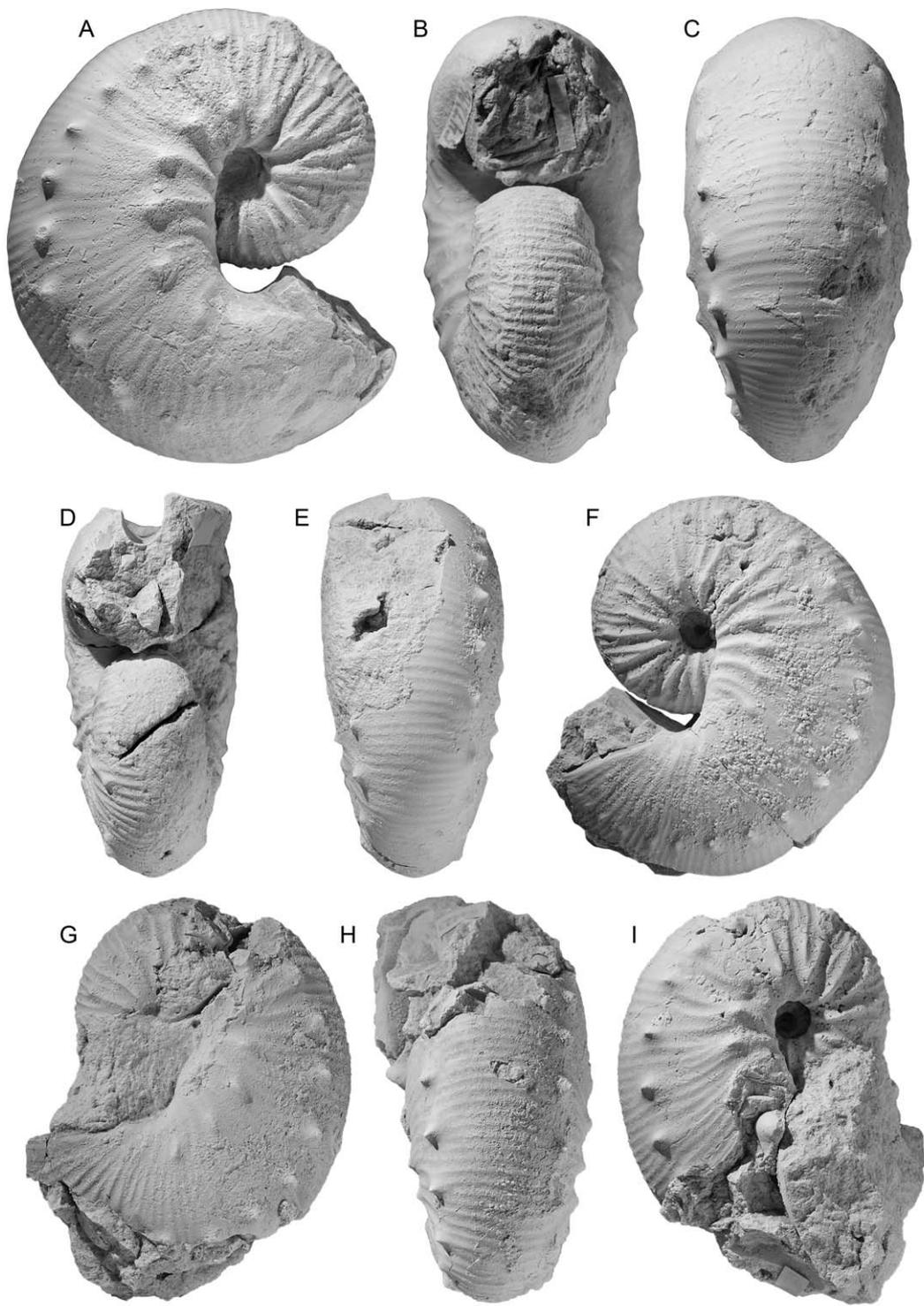
spaced on the adoral part, where they attain their maximum height. They subsequently diminish in size and spacing toward the aperture. In the largest specimen, USNM 547296, the maximum distance between consecutive bullae on the body chamber is 9 mm (fig. 9A–C). One or two ribs join a bulla dorsally, and two to four ribs branch from it ventrally. As many as two ribs intercalate between bullae.

Ventrolateral tubercles appear on the shell anywhere from the point of exposure, as in USNM 547298 (fig. 6D, E), to the adoral end of the phragmocone, as in USNM 547295 (fig. 7C–E). Very rarely are they absent altogether on the phragmocone, as in USNM 547301 (fig. 7I–K). They are relatively small on the phragmocone, less than 1.5 mm in height. In general, they are unevenly spaced with gaps between successive tubercles. For example, in USNM 547295 (fig. 7C–E), starting at the point of exposure, the distance between successive tubercles, as measured in an adoral direction, is 3, 3, 3, 5.5, 3, 6, and 7.5 mm. The distribution is also uneven in USNM 547300 (fig. 7P, Q). Starting at the point of exposure, the distance between successive tubercles, as measured in an adoral direction, is 5, 5, 6, 6.5, and 4.5 mm. More rarely, the tubercles on the phragmocone become gradually more widely spaced in an adoral direction. For example, in USNM 547296 (fig. 9A–C), starting midway on the exposed phragmocone, the distance between successive tubercles gradually increases, attaining a maximum value of 6.5 mm at the adoral end of the phragmocone. The maximum total number of ventrolateral tubercles on the exposed phragmocone is 12. One or two ribs join a ventrolateral tubercle dorsally and two or three ribs branch from it ventrally, looping to ventrolateral tubercles on the opposite side of the venter. As many as five ribs intercalate between ventrolateral tubercles, depending on the distance between tubercles and the density of ribbing.

Ventrolateral tubercles are invariably present on the body chamber and occur at 85%–90% whorl height. In a few specimens, such as the holotype, the largest gap between ventrolateral tubercles occurs between the most adoral tubercle on the phragmocone and the most adapical tubercle on the body chamber. Thereafter, the tubercles are nearly always more or less uniformly spaced. For example, in USNM 547302 (fig. 6Y, Z), starting at the adapical end of the body chamber, the distance between successive tubercles, as measured in an adoral direction, is nearly constant (6.5, 5, 5, 5.5, 5.5, and 6 mm). The distribution of ventrolateral tubercles on the body chamber is also nearly uniform in USNM 547293 (fig. 6Q, R). Starting at the adapical end of the body chamber, the distance between successive tubercles, as measured in an adoral direction, is 4.5, 4.5, 4, 5, 5, 3.5, and 5 mm.

Ventrolateral tubercles attain their maximum height at midshaft (1.5 mm). In some specimens, the tubercles become weakly clavate at this point, with a flat, steepened adapical face, and a more gently sloping adoral face. In smaller, more finely ornamented specimens such as the holotype, the ventrolateral tubercles die out on the adoral end of the shaft. In larger, more

FIG. 8. *Hoploscaphites gilberti*, n. sp., macroconchs. A–C. USNM 547304, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D379, El Paso County, Colorado. A, Right lateral; B, ventral; C, apertural. D, E. Sc 590A, cast, *Didymoceras nebrascense* Zone, Pierre Shale, Fall River County, South Dakota. D, Right lateral; E, ventral. F. USNM 547294, right lateral, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D84, Pueblo County, Colorado. G–I. USNM 547292, *Didymoceras nebrascense* Zone, Pierre shale, USGS Mesozoic loc. D13538, Weston County, Wyoming. G, Right lateral; H, apertural; I, ventral. Specimens $\times 1$.



coarsely ornamented specimens such as USNM 547294 (fig. 8F), the ventrolateral tubercles persist onto the hook, where they become smaller, more bullate, and more closely spaced. The total number of ventrolateral tubercles on the body chamber ranges from 6 to 14 (8 in the holotype). The total number of ventrolateral tubercles on the entire adult shell ranges from 6 to 21 (8 in the holotype). At midshaft, one to three ribs join a ventrolateral tubercle dorsally and two or three ribs branch from it ventrally, looping between ventrolateral tubercles on the opposite side of the venter. Two to four ribs intercalate between ventrolateral tubercles, depending on the distance between tubercles and the density of ribbing.

The suture is simple, with a broad, asymmetrically bifid first lateral saddle (E/L) and a narrow, symmetrically to asymmetrically bifid first lateral lobe (L) (fig. 12).

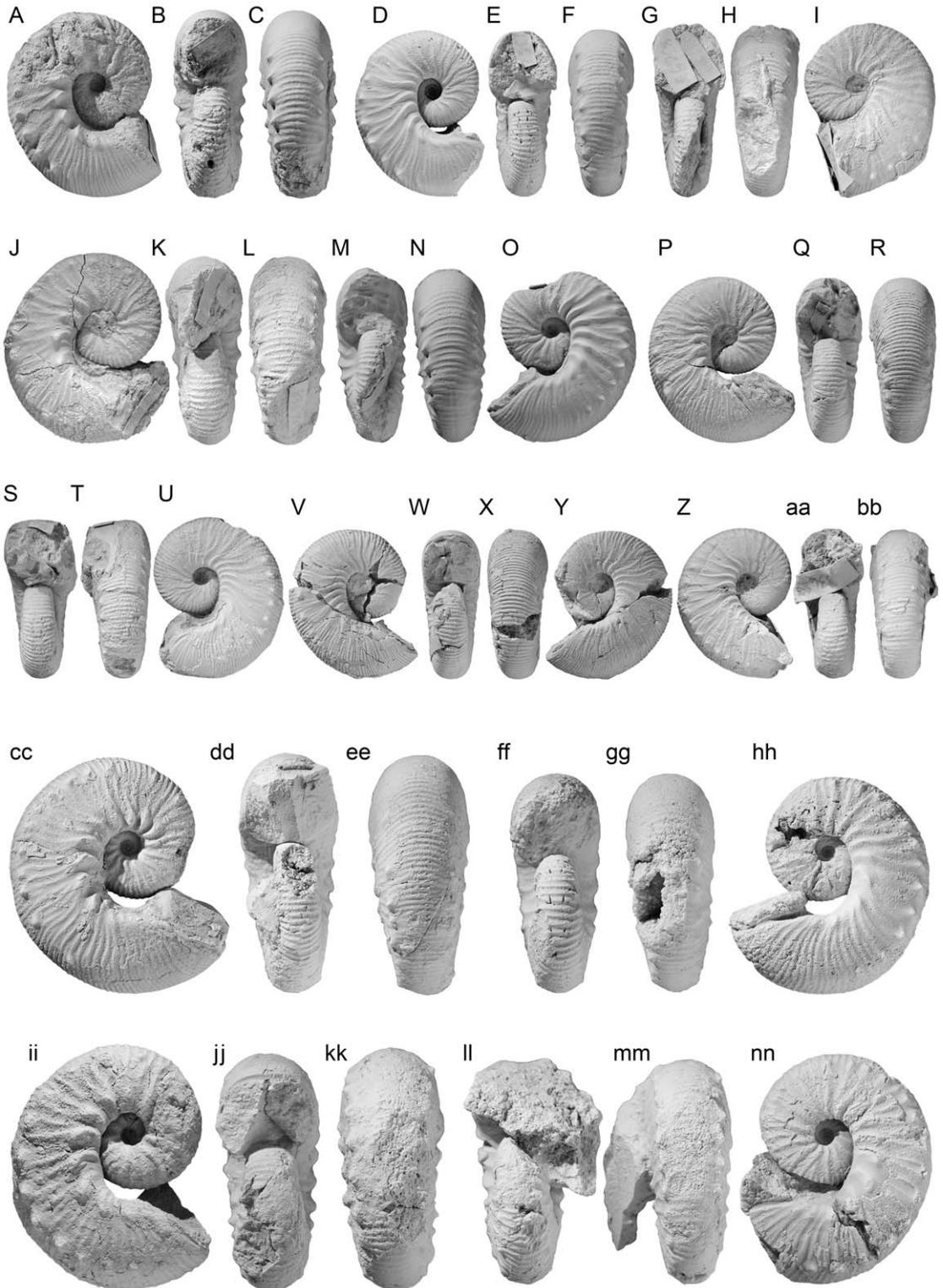
MICROCONCH DESCRIPTION: L_{MAX} averages 32.9 mm and ranges from 23.8 to 44.1 mm (table 3). The size distribution is unimodal, with a peak at 30–35 mm (fig. 4). The ratio of the size of the largest specimen to that of the smallest is 1.85. The size distribution of macroconchs and microconchs overlaps. The average size of microconchs is 77% that of macroconchs. The size range of microconchs is reduced in samples from single localities (fig. 5). At USGS Mesozoic loc. D3935, L_{MAX} ranges from 23.8 to 36.0 mm; the ratio of the size of the largest specimen to that of the smallest is 1.51. At AMNH loc. 3386, L_{MAX} ranges from 26.4 to 39.8 mm; the ratio of the size of the largest specimen to that of the smallest is also 1.51.

Shells range from circular to elongate in lateral view, clustering more heavily on the elongate end of the spectrum. The exposed phragmocone occupies one-half to two-thirds of a whorl. In general, the base of the body chamber occurs below the line of maximum length. The umbilicus of the phragmocone is relatively small. UD average 3.60 mm and UD/L_{MAX} averages 0.11. The body chamber consists of a relatively long shaft and recurved hook, leaving a small gap between the exposed phragmocone and hook. The ratio of L_{MAX}/H_p averages 3.33, which is greater than that in macroconchs (3.13), implying that microconchs are relatively more uncoiled than macroconchs. The apertural lip is flexuous, with a short dorsal projection. The umbilical seam of the shaft is concave in lateral view revealing the umbilicus of the phragmocone. The curvature of the seam closely matches that of the venter, epitomizing the morphology of microconchs.

The intercostal whorl section of the phragmocone along the line of maximum length is compressed subquadrate. W_p/H_p averages 0.90 (0.90 also in macroconchs). The umbilical wall is steep and subvertical and the umbilical shoulder is sharply rounded. The inner flanks are broadly rounded and the outer flanks are nearly flat and converge toward the venter. Maximum width occurs at one-third whorl height. The ventrolateral margin is sharply rounded and the venter is more broadly rounded.

Whorl width and height gradually increase as the shell passes into the shaft. Whorl width attains its maximum value at the point of recurvature, and whorl height attains its maximum

FIG. 9. *Hoploscaphites gilberti*, n. sp., macroconchs. A–C. USNM 547296, paratype, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3464, Pueblo County, Colorado. A, Right lateral; B, apertural; C, ventral. D–F. AMNH 64699, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. D, Apertural; E, ventral; F, left lateral. G–I. AMNH 64423, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. G, Left lateral; H, ventral; I, right lateral. Specimens $\times 1$.



value at midshaft. The increase in whorl height from the phragmocone to the shaft is much more gradual than that in macroconchs.

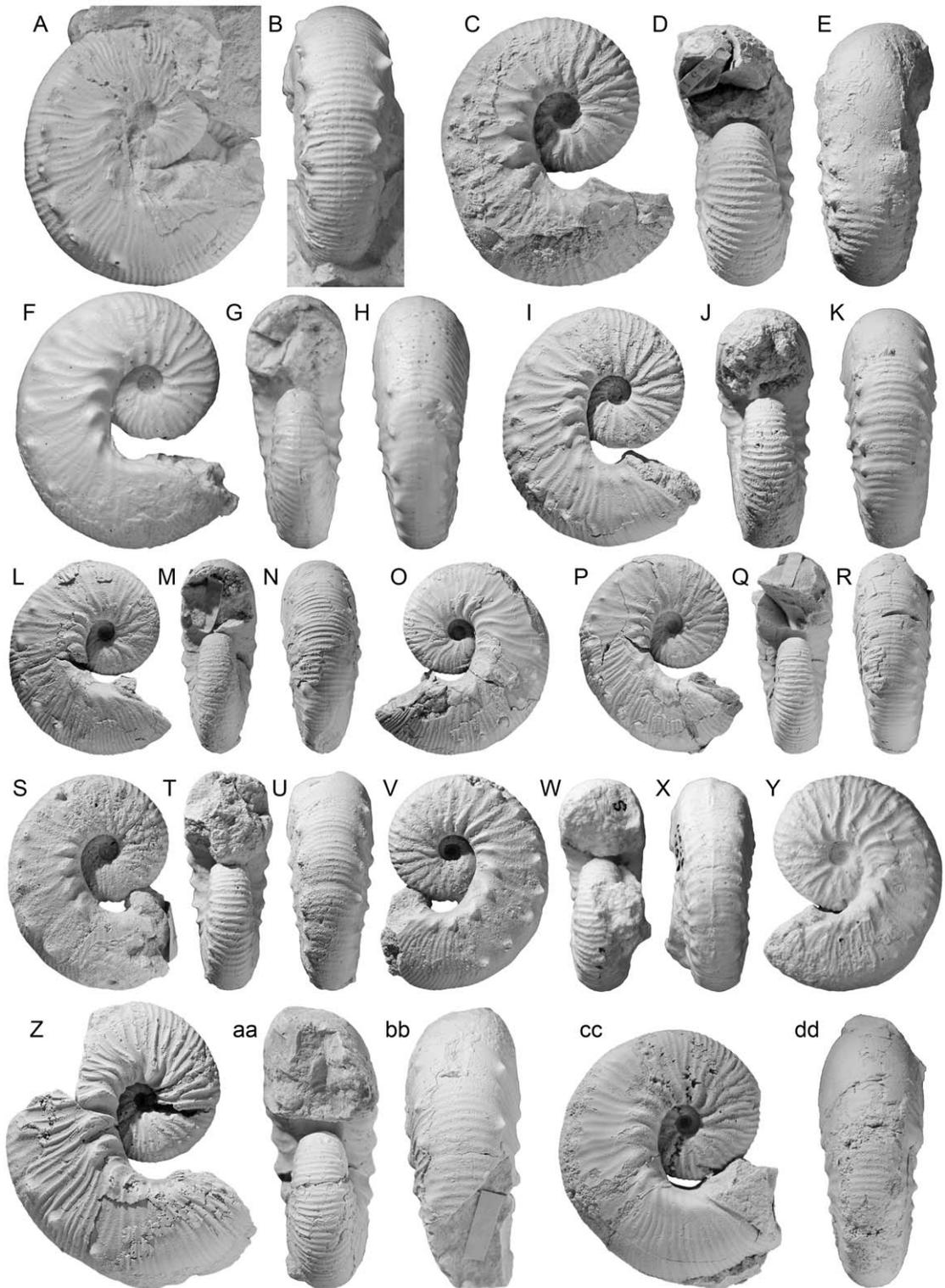
The whorl section at midshaft exhibits nearly the same degree of compression as that of the phragmocone along the line of maximum length (W_S/H_S averages 0.90). The ratio of V_S/H_S averages 0.68 and ranges from 0.55 to 0.83. The intercostal whorl section is subquadrate with maximum width at one-quarter whorl height, corresponding to the site of the umbilicolateral bullae. The umbilical wall is steep and the umbilical shoulder, unlike that in macroconchs, slopes gently outward. The flanks are broadly rounded to flat and converge toward the venter. The ventrolateral shoulder is sharply rounded and the venter is more broadly rounded.

As in macroconchs, the whorl section becomes slightly less compressed from midshaft to the point of recurvature, after which it remains nearly the same. W_H/H_H averages 1.02. The intercostal whorl section at the point of recurvature is slightly more ovoid than that at midshaft. The umbilical wall is nearly flat and the umbilical shoulder is sharply rounded. The flanks are broadly rounded, with maximum width at one-third whorl height. The ventrolateral shoulder is sharply rounded and the venter is more broadly rounded.

The ornament in microconchs is similar to that in macroconchs. Specimens are covered with relatively fine, flexuous ribs, and rows of umbilicolateral bullae and ventrolateral tubercles. However, in many small specimens, these latter features only appear on the shaft of the body chamber.

At the point of exposure, ribs are rursiradiate on the umbilical wall and shoulder. They are prorsiradiate and slightly flexuous on the flanks, swinging slightly backward on the inner flanks, slightly forward on the midflanks, and slightly backward again on the outer flanks, crossing the venter with a slight forward projection. Branching and intercalation occur at one-third and two-thirds whorl height, at the umbilicolateral and ventrolateral margin, respectively. The rib density on the phragmocone along the line of maximum length ranges from 9 to 11

FIG.10. *Hoploscaphites gilberti*, n. sp., microconchs. **A–C**. AMNH 64575, AMNH loc. 3386, *Baculites scotti* Zone, Pierre Shale, Butte County, South Dakota. A, Right lateral; B, apertural; C, ventral. **D–F**. USNM 547344, Pierre Shale, USGS loc. 1362, Pueblo County, Colorado. D, Right lateral; E, apertural; F, ventral. **G–I**. USNM 547314, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. G, Apertural; H, ventral; I, left lateral. **J–L**. USNM 547320, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. J, Right lateral; K, apertural; L, ventral. **M–O**. USNM 547330, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D1509, Pueblo County, Colorado. M, Apertural; N, ventral; O, left lateral. **P–R**. USNM 547322, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D8551, El Paso County, Colorado. P, Right lateral; Q, apertural; R, ventral. **S–U**. USNM 547317, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. S, Apertural; T, ventral; U, left lateral. **V–Y**. USNM 547326, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. V, Right lateral; W, apertural; X, ventral; Y, left lateral. **Z–bb**. USNM 547310, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. Z, Right lateral; aa, apertural; bb, ventral. **cc–ee**. USNM 547324, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D8271, Pueblo County, Colorado. cc, Right lateral; dd, apertural; ee, ventral. **ff–hh**. AMNH 81467, paratype, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. ff, Apertural; gg, ventral; hh, left lateral. **ii–kk**. AMNH 63538, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3494, Weston County, Wyoming. ii, Right lateral; jj, apertural; kk, ventral. **ll–nn**. AMNH 64536, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3494, Weston County, Wyoming. ll, Apertural; mm, ventral; nn, left lateral. Specimens $\times 1$.



ribs/cm except in very small specimens such as USNM 547326 (fig. 10V–Y) in which the density is as high as 16 ribs/cm.

On the body chamber, primary ribs arise at the umbilical seam and are strong on the umbilical wall. They are narrow and weakly flexuous on the flanks, bending slightly backward on the inner flanks, slightly forward on the midflanks, and slightly backward again on the outer flanks. Ribs are rectiradiate on the adapical end of the shaft, becoming more prorsiradiate on the adoral end of the shaft. Branching and intercalation occur at the umbilicolateral margin (at the bullae if they are present) and at the ventrolateral margin (at and between the ventrolateral tubercles). Ribs cross the venter with a weak adoral projection. The rib density at midshaft ranges from 12 to 16 ribs/cm, with the exception of 22 ribs/cm in USNM 547326 (fig. 10V–Y), and remains the same or increases slightly on the hook.

Umbilicolateral bullae are absent on the phragmocone in small specimens and, instead, the ribs in this area are strong and adorally concave. Even in large specimens, as in USNM 547324 (fig. 10cc–ee), umbilicolateral bullae appear only on the adoral one-third of the phragmocone. They occur at one-third whorl height and are linked to the umbilicus by strong primary ribs. The bullae are more or less evenly spaced with a maximum distance of 3 mm between them. One rib joins a bulla dorsally, and two ribs branch from it ventrally. One or two ribs intercalate between bullae.

Umbilicolateral bullae are always present on the body chamber, with the exception of very small specimens such as USNM 547314 (fig. 10G–I). The maximum total number of umbilicolateral bullae on the body chamber is 6, and the maximum total number of bullae on the adult shell is 9. The bullae occur at one-quarter whorl height on the shaft, but migrate closer to the umbilical shoulder on the hook. They are small and attain their maximum height (1.5 mm) on the adoral end of the shaft. They are more or less evenly spaced, with some approximation near the aperture. For example, in USNM 547324 (fig. 10cc–ee), the bullae are nearly uniformly spaced at intervals of 3–4 mm. At midshaft, one rib joins an umbilicolateral bulla dorsally and two or three ribs branch from it ventrally. One or two ribs intercalate between successive bullae.

Ventrolateral tubercles are present on the exposed phragmocone in nearly all of the specimens in our sample. The maximum total number of tubercles on the exposed phragmocone is 9, but such a high number is rare, with most specimens exhibiting only 2 to 7 tubercles. In

FIG. 11. *Hoploscaphites gilberti*, n. sp., microconchs. **A, B.** Sc 685B, cast, *Didymoceras nebrascense* Zone, Pierre Shale, Fall River County, South Dakota. **A**, Right lateral; **B**, ventral. **C–E.** USNM 547603, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D8551, El Paso County, Colorado. **C**, Right lateral; **D**, apertural; **E**, ventral. **F–H.** Sc 1289A, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. **F**, Right lateral; **G**, apertural; **H**, ventral. **I–K.** AMNH 64615, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **I**, Right lateral; **J**, apertural; **K**, ventral. **L–O.** USNM 547325, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. **L**, Right lateral; **M**, apertural; **N**, ventral; **O**, left lateral. **P–R.** USNM 547306, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D3935, Pueblo County, Colorado. **P**, Right lateral; **Q**, apertural; **R**, ventral. **S–V.** AMNH 64573, paratype, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **S**, Right lateral; **T**, apertural; **U**, ventral; **V**, left lateral. **W–Y.** USNM 28362, paratype, cast, Pierre Shale, USGS loc. 1359, Pueblo County, Colorado (Gilbert, 1896: pl. 63, fig. 3). **W**, Apertural; **X**, ventral; **Y**, left lateral. **Z–bb.** AMNH 81118, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. **Z**, right lateral; **aa**, apertural; **bb**, ventral. **cc, dd.** USNM 547335, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D285, Douglas County, Colorado. **cc**, Right lateral; **dd**, ventral. Specimens $\times 1$.

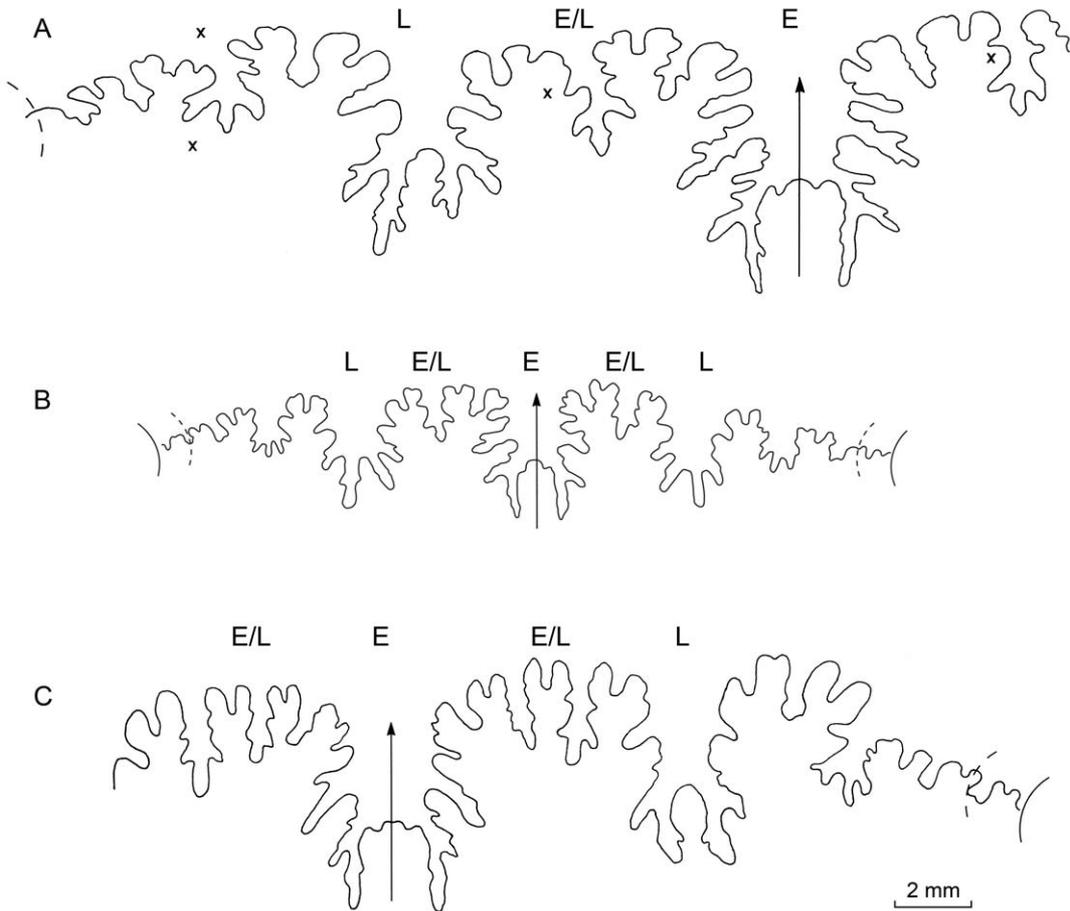


FIG. 12. Sutures of *Hoploscaphites gilberti*, n. sp., and *H. gilli* Cobban and Jeletzky, 1965. **A.** *H. gilberti*, n. sp., USNM 547302, macroconch, last suture, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D1509, Pueblo County, Colorado. **B.** *H. gilberti*, n. sp., USNM 547344, microconch, next to last suture, *Baculites scotti* Zone, Pierre Shale, USGS Mesozoic loc. D1362, Pueblo County, Colorado. **C.** *H. gilli*, USNM 547334, macroconch, third from last suture, *Baculites gregoryensis* Zone, Pierre Shale, USGS Mesozoic loc. D1900, Niobrara County, Wyoming. Abbreviations: x, tubercle; E, ventral lobe; E/L, first lateral saddle between ventral and lateral lobes; L, lateral lobe.

general, tubercles appear between the middle and adoral end of the phragmocone. They are unevenly spaced with gaps between them. For example, in AMNH 81467 (fig. 10ff–hh), starting near the point of exposure, the distance between successive tubercles, as measured in an adoral direction, is 2, 2.5, 2.5, 5.5, 3, and 2.5 mm. Commonly, one rib joins a ventrolateral tubercle dorsally and two ribs branch from it ventrally, looping to ventrolateral tubercles on the opposite side of the venter, with one to three intercalated ribs between them.

Ventrolateral tubercles are invariably present on the shaft, but rarely continue onto the hook. They are less than 1.5 mm in height, and are smaller than the adjacent umbicolateral bullae. They occur at 90% whorl height and are paired or offset from one side of the venter to

the other. They are more or less uniformly spaced although gaps are not uncommon, especially at the adapical and adoral ends of the shaft. For example, in USNM 547324 (fig. 10cc–ee), the distance between consecutive tubercles, as measured in an adoral direction, is 4, 3.5, 3.5, 3.5, 4.5, 3, 5.5, and 8.5 mm. The total number of ventrolateral tubercles on the body chamber ranges from 5 to 12, and the total number of tubercles on the entire adult shell ranges from 9 to 16. One to three ribs join a ventrolateral tubercle dorsally and two to four ribs branch from it ventrally. Three to six ribs intercalate between tubercles, depending on the density of ribbing and the spacing between tubercles.

The suture of microconchs is similar to that of macroconchs (fig. 12).

JAWS AND HOOKLIKE STRUCTURES: AMNH locs. 3340 and 3386 contain abundant jaws and hooklike structures (fig. 13). The jaws appear as isolated occurrences and are attributed to *Hoploscaphites gilberti*, n. sp., or an as yet undescribed, more coarsely ornamented species of *Hoploscaphites*. The lower jaw conforms to the structural plan of the *Aptychophora* (Landman et al., 2010). It consists of two symmetrical wings separated by a slit down the middle (fig. 13A). The upper jaw consists of a pair of widely open inner lamellae and a short, reduced outer lamella, both of which converge toward the apex (fig. 13B).

The hooklike structures are approximately 2 mm in maximum length and are composed of the same black material as the jaws, presumably originally chitin (fig. 13C–E). The most complete specimens consist of two hollow projecting points extending from a bulbous base. These structures have been documented in other species of *Hoploscaphites* by Landman and Waage (1993). Similar but much larger structures have also been described in *Rhaeboceras* by Kennedy et al. (2002). The function of these structures is unknown.

DISCUSSION: In his description of the Pierre Shale of Colorado, Gilbert (1896: pl. 63, fig. 3) illustrated a specimen of what he called a small variety of *Scaphites nodosus* (USNM 28362). It is from a limestone core of a tepee butte in the Pierre Shale at USGS loc. 1359, Pueblo County, Colorado, and a microconch of *Hoploscaphites gilberti*, n. sp. (fig. 11W–Y). Gilbert (1896: pl. 65, fig. 2) also illustrated a specimen of what he called a large individual of *S. nodosus* (USNM 28363). It is from the Hygiene Sandstone Member of the Pierre Shale of Colorado (what he called the “Tepee zone of the Pierre Shale”). This specimen is a macroconch of an as yet undescribed closely related species of *H. nodosus* from the *Baculites reesidei* Zone.

Hoploscaphites gilberti, n. sp., most closely resembles *H. gilli* Cobban and Jeletzky, 1965, which ranges from the *Baculites perplexus* to *Didymoceras stevensoni* zones of the Western Interior of North America (middle middle to lower upper Campanian). Indeed, Cobban and Jeletzky (1965: pl. 95, fig. 1A–D) illustrated what they described as a coarsely ornamented specimen of *H. gilli* from southeastern Montana on the northwestern flanks of the Black Hills, which is actually a microconch of *H. gilberti*, n. sp. Several morphological features distinguish *H. gilberti*, n. sp., from *H. gilli* (fig. 14). In terms of the whorl cross section, the flanks of the body chamber are nearly subparallel in *H. gilberti*, n. sp., whereas they are more steeply convergent toward the venter in *H. gilli*. In terms of ornamentation, the two species differ in the density of ribbing, with *H. gilberti*, n. sp., having more widely spaced ribs. For example, the density of ribbing on the midshaft of the holotype of *H. gilberti*, n. sp., is 10 ribs/cm whereas

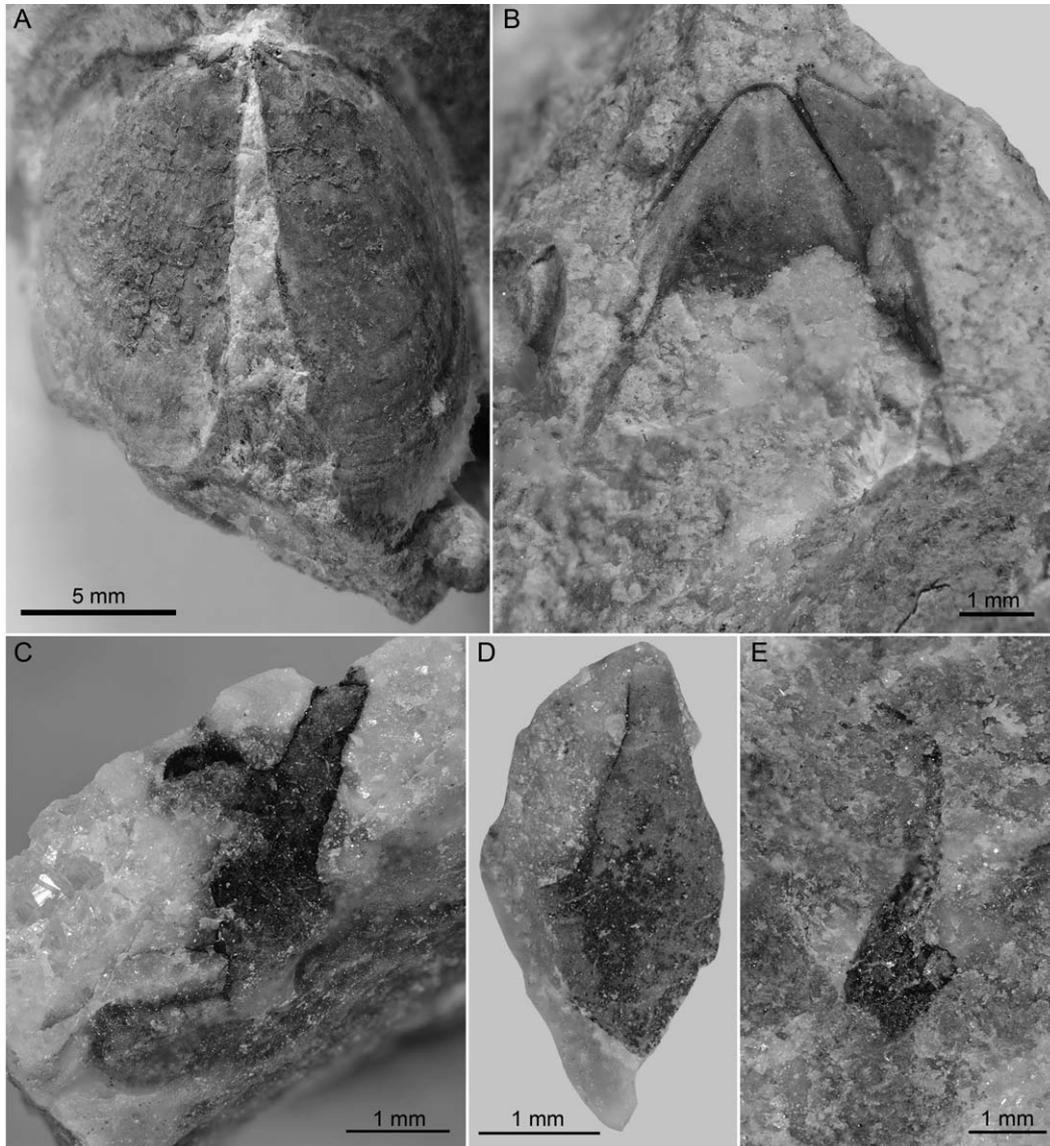


FIG. 13. Jaws and hooklike structures attributed to *Hoploscaphites gilberti*, n. sp., or an as yet undescribed, more coarsely ornamented species of *Hoploscaphites*, Pierre Shale, South Dakota. **A.** Lower jaw showing the midline slit, ventral view, apex on top, AMNH 64532, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **B.** Upper jaw, apex on top, AMNH 64547, *Baculites scotti* Zone, Pierre Shale, AMNH loc. 3386, Butte County, South Dakota. **C.** Hooklike structure showing one of the points projecting to the upper right, AMNH 63530, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3440, Butte County, South Dakota. **D.** Hooklike structure with the basal portion exposed on the bottom, AMNH 63531, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota. **E.** Hooklike structure with one point complete and one point broken, AMNH 64533, *Didymoceras nebrascense* Zone, Pierre Shale, AMNH loc. 3340, Fall River County, South Dakota.

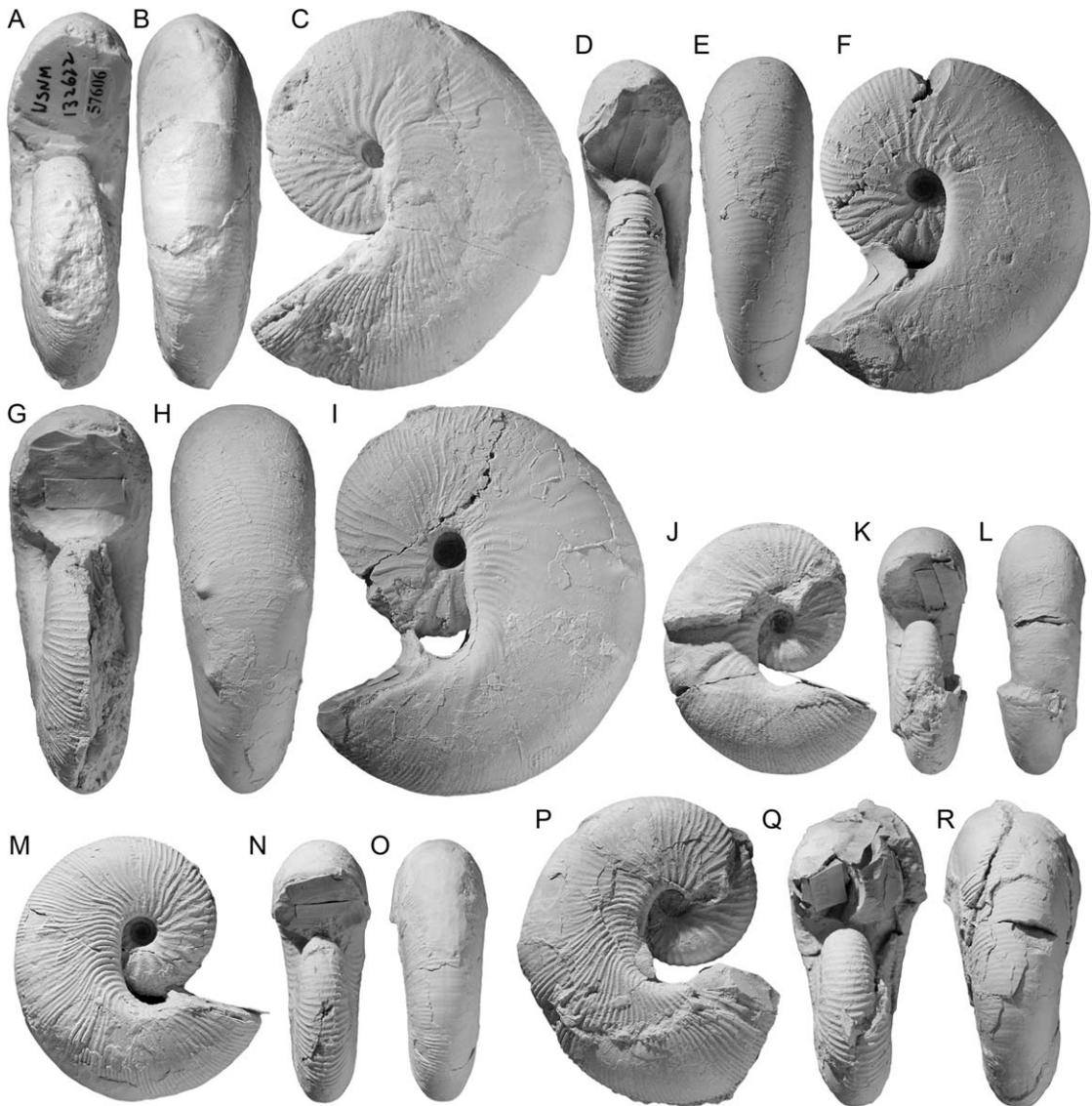


FIG. 14. *Hoploscaphites gilli* Cobban and Jeletzky, 1965. A–C. USNM 132622, macroconch, cast, Pierre Shale, USGS Mesozoic loc. D1871, Niobrara County, Wyoming. A, Apertural; B, ventral; C, left lateral. D–F. USNM 547334, macroconch, *Baculites gregoryensis* Zone, Pierre Shale, USGS Mesozoic loc. D1900, Niobrara County, Wyoming. D, Apertural; E, ventral; F, left lateral. G–I. USNM 547333, macroconch, *Baculites gregoryensis* Zone, Pierre Shale, USGS Mesozoic loc. D1900, Niobrara County, Wyoming. G, Apertural; H, ventral; I, left lateral. J–L. USNM 547600, microconch, *Baculites perplexus* Zone, Pierre Shale, USGS Mesozoic loc. D264, Douglas County, Colorado. J, Right lateral; K, apertural; L, ventral. M–O. USNM 547601, microconch, *Baculites perplexus* Zone, Pierre Shale, USGS Mesozoic loc. D398, Crook County, Wyoming. M, Right lateral; N, apertural; O, ventral. P–R. USNM 547602, microconch, *Baculites perplexus* Zone, Cody Shale, USGS Mesozoic loc. D255, Converse County, Wyoming. P, Right lateral; Q, apertural; R, ventral. Specimens $\times 1$. For locality information, see Cobban and Jeletzky (1965).

it is 13 ribs/cm on the midshaft of a macroconch of *H. gilli* of comparable size (fig. 14D–F). In addition, *H. gilberti*, n. sp., bears umbilicolateral bullae on the body chamber whereas these features are absent in *H. gilli*. In contrast, ventrolateral tubercles are present on the body chamber of both species, although they are larger, more numerous, and more closely spaced in *H. gilberti*, n. sp., than in *H. gilli*.

Hoploscaphites gilberti, n. sp., is also similar to *H. brevis* Meek, 1876, which ranges from the *Didymoceras cheyennense* to *Baculites cuneatus* zones of the Western Interior of North America (middle upper Campanian). However, the venter at midshaft is more rounded in *H. gilberti*, n. sp., than in *H. brevis*. As a result, the distance between ventrolateral tubercles on either side of the venter is greater in *H. gilberti*, n. sp., than in *H. brevis*. For example, the value of V_s/H_s , which is a relative measure of the distance between ventrolateral tubercles on either side of the venter, averages 0.62 in our sample of 14 macroconchs of *H. gilberti*, n. sp., versus 0.43 in a sample of 54 macroconchs of *H. brevis*, as recorded in Landman et al. (2010: table 7).

Hoploscaphites gilberti, n. sp., is strongly dimorphic, with the dimorphs referred to as macroconchs (figs. 6–9) and microconchs (figs. 10, 11). The dimorphs are interpreted as sexual in nature, the macroconchs female, and the microconchs male, following the traditional view as outlined by Makowski (1962) and Cobban (1969). Dimorphs are distinguished at maturity by the presence of an umbilical bulge, the outline of the umbilical shoulder relative to that of the venter in side view, the size of the umbilical diameter, the change in whorl height from the mature phragmocone to the midshaft of the body chamber, and adult size.

Some of these criteria are more reliable than others in distinguishing between dimorphs. For example, the size of the largest macroconch is larger than the size of the largest microconch, but the size distributions of the two dimorphs overlap. In addition, the curvature of the umbilical seam is not an infallible indicator of the dimorph. In some specimens, the umbilical shoulder is straight, suggesting a macroconch, but other features of the shell, including a gradual rather than abrupt increase in whorl height in passing from the phragmocone to the midshaft, suggest a microconch instead. Landman et al. (2010) called such specimens “microconchs, transitional to macroconchs.” In our sample of *Hoploscaphites gilberti*, n. sp., we classify AMNH 81100 (fig. 6I–K) as a macroconch because it exhibits a straight umbilical shoulder. However, the increase in whorl height in passing from the phragmocone to the midshaft is less abrupt than that in most macroconchs, and, as a result, the shell is more elongate.

Hoploscaphites gilberti, n. sp., shows a broad range in adult size. In macroconchs, L_{MAX} ranges from 27.9 to 79.8 mm, and, in microconchs, it ranges from 23.8 to 39.8 mm. Most of our specimens are from cold methane seep deposits in the *Baculites scotti* and overlying *Didymoceras nebrascense* zones of the Pierre Shale. However, three of the largest specimens, USNM 547304 (fig. 8A–C), 547296 (fig. 9A–C), and Sc 590A (fig. 8D, E) are from age-equivalent nonseep sites. It is possible that the variation in adult size between sites may reflect differences in the timing of maturation. Assuming that all specimens grew at approximately the same rate, the smaller size of the specimens from the seeps may indicate that they matured at a smaller size due to the abundant supply of nutrients at these sites.

OCCURRENCE: This species occurs in the *Baculites scotti* and overlying *Didymoceras nebrascense* zones (upper middle to lower upper Campanian) of the U.S. Western Interior. It is especially common in the tepee buttes along the Front Range of Colorado and the Black Hills region of South Dakota, Wyoming, and Montana. These sites represent deposits associated with cold methane seeps (Gilbert and Gulliver, 1895; Kauffman et al., 1996; Landman et al., 2012).

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APPENDIX

LIST OF LOCALITIES

Localities are numbered consecutively and mapped in figure 1. Localities 1–23 are U.S. Geological Survey (USGS) localities. The prefix D refers to Denver locality numbers and the others refer to Washington D.C. numbers. The names of collectors and dates of collection are indicated at the end of each entry. Localities 24–31 are American Museum of Natural History (AMNH) localities.

1. 750. Pierre Shale, northeast of Pueblo, 38°20'8" N, 104°31'42"W, Pueblo County, Colorado. T.W. Stanton, 1890.
2. 1359. Pierre Shale, north of Boone, 38°15'N, 104°13–18'W, Pueblo County, Colorado. G.K. Gilbert, 1894.
3. 1362. Pierre Shale, north fork of Salt Creek, 38°26'59"N, 104°22'58"W, Pueblo County, Colorado. G.K. Gilbert, 1894.
4. D84. *Baculites scotti* Zone, G.K. Gilbert's "Tepee zone" of Pierre Shale, southeast end of Baculite Mesa, 4.5 mi (7.2 km) northeast of Pueblo, SE1/4 sec. 3, T. 20 S., R. 64. W., Pueblo County, Colorado. G.R. Scott, G.E. Lewis, and W.A. Cobban, 1954.
5. D85. *Baculites scotti* Zone, G.K. Gilbert's "Tepee zone" of Pierre Shale, same locality as D84.
6. D285, *Baculites scotti* Zone, Pierre Shale, from a tepee butte 1.5 mi (1.0 km) southeast of Kassler, SW1/4 NW1/4 NW1/4 sec. 1, T. 7 S., R. 69 W., Douglas County, Colorado.
7. D379. *Baculites scotti* Zone, upper 25 ft (7.6 m) of G.K. Gilbert's *Baculites* Zone of Pierre Shale, hillside 0.25 mi (0.4 km) east of Fountain Creek and 0.5 mi (0.8 km) south-southeast of Little Buttes, NE1/4NE1/4 sec. 4, T. 17 S., R. 65 W., El Paso County, Colorado. W.A. Cobban, 1964.
8. D1260. Top of *Baculites scotti* Zone, Tepee limestone and rusty ironstones, Pierre Shale, 8.0 mi (12.9 km) north-northeast of Pueblo, SE1/4SE1/4 sec. 9, T. 19 S., R. 64W., Pueblo County, Colorado. G.R. Scott and W.A. Cobban, 1957.
9. D1507. *Baculites scotti* Zone, small gray limestone concretions, Pierre Shale, west side of Baculite Mesa, SE1/4NW1/4 and NE1/4SW1/4 sec. 4, T. 20S., R. 64W., Pueblo County, Colorado. G.R. Scott and W.A. Cobban, 1957.
10. D1508. *Baculites scotti* Zone, Pierre Shale, same level as D1507, south end of Baculite Mesa, NE1/4NE1/4 sec. 9, T. 20S., R. 64W., Pueblo County, Colorado. G.R. Scott and W.A. Cobban, 1957.
11. D1509. *Baculites scotti* Zone, Pierre Shale, higher than D1508 and a little north, south end of Baculite Mesa, NE1/4NE1/4 sec. 9, T. 20S., R. 64W., Pueblo County, Colorado. G.R. Scott and W.A. Cobban, 1957.
12. D1802. *Baculites scotti* Zone, Pierre Shale, tepee butte limestone, NW1/4NW1/4 sec. 4, T. 19S., R. 64W. (38°25'36.5"N, 104°33'43.6"W), Pueblo County, Colorado. G.R. Scott, 1958.
- D1803. *Didymoceras nebrascense* Zone, Pierre Shale, a tepee butte a little higher than D1802, NW1/4NW1/4 sec. 4, T. 19S., R. 64W. (38°25'36.5"N, 104°33'43.6"W), Pueblo County, Colorado. G.R. Scott, 1958.

13. D2621. *Baculites scotti* Zone, Pierre Shale, above the Mitten Member of the Pierre Shale, NW1/4NW1/4NE1/4 sec. 17, T. 45N., R. 62W. (43°54'28.0"N, 104°18'32.9"W), Weston County, Wyoming. W.J. Mapel and C. Pillmore, 1960.
14. D2629. *Didymoceras nebrascense* Zone, Hygiene Sandstone Member of the Pierre Shale, SW1/4NE1/4 NE1/4 sec. 34, T. 2N., R. 78W. (40°5'36.4"N, 106°6'70.8"W), Grand County, Colorado. W.R. Brown, 1957.
15. D2792. *Baculites scotti* Zone, Pierre Shale, SE1/4SW1/4SE1/4NE1/4 sec. 6, T. 1N., R. 70W. (40°4'51.8"N, 105°16'20.2"W), Boulder County, Colorado. G.R. Scott, 1960.
16. D3464. *Baculites scotti* Zone, Pierre Shale, maroon limestone concretion in silty grey shale, roadcut of US 85 and 87, NE1/4NW1/4NE1/4 sec. 2, T. 18S., R. 65W., Pueblo County, Colorado. G.R. Scott and family, 1961.
17. D35--. *Baculites scotti* Zone, Pierre Shale, locality unknown (label is partly torn off of specimen), but probably El Paso County, Colorado.
18. D3935. *Baculites scotti* Zone, Pierre Shale, NE1/4NW1/4 sec 10, T. 20S., R. 64W., northeast of Pueblo, Pueblo County, Colorado. G.R. Scott and J. Scott. 1962.
19. D3936. *Baculites scotti* Zone, Pierre Shale, NE1/4NE1/4 sec. 10, T. 20S., R. 64W. (38°19'33"N, 104°32'37.2"W), Pueblo County, Colorado. G.R. Scott and J. Scott, 1962.
20. D3941. *Baculites scotti* Zone, Pierre Shale, SW1/4SE1/4 sec. 35, T. 19S. R. 64W., Pueblo County, Colorado. G.R. Scott, 1962.
21. D8550. *Baculites scotti* Zone, Pierre Shale, NW1/4SE1/4 sec. 28, T. 17S., R. 65W. (38°32'32"N, 104°40'22"W), El Paso County, Colorado. G.R. Scott and J. Scott, 1971.
D8551. *Baculites scotti* Zone, Pierre Shale, SW1/4SE1/4 NW1/4 sec. 3, T. 18S., R. 65W., El Paso County, Colorado. G.R. Scott, 1971.
22. D8271. *Baculites scotti* Zone, Pierre Shale, SE1/4NE1/4SE1/4 sec. 17, T. 18S., R. 64W. (38°29'4.3"N, 104°34'50.0"W), Pueblo County, Colorado. G.R. Scott and J. Scott, 1972.
23. D13538. Upper part of *Didymoceras nebrascense* Zone, tepee butte, Pierre Shale, near center of E1/2 sec. 13 T. 45N., R. 63 W., Weston County, Wyoming. W.A. Cobban, 1994.
24. AMNH loc. 3332. *Didymoceras nebrascense* Zone (possibly slightly above this zone), seep, Pierre Shale, NW1/4 sec. 11, T. 17S., R. 65W., El Paso County, Colorado.
25. AMNH loc. 3340. *Didymoceras nebrascense* Zone, seep, Pierre Shale, NW1/4 SW1/4NW1/4SW1/4NE1/4 sec. 12, T. 7S., R. 7E., near Buffalo Gap, Fall River County, South Dakota.
26. AMNH loc. 3342. *Didymoceras nebrascense* Zone, seep, Pierre Shale, SW1/4 sec. 2, T. 8S., R. 7E., near Oral, Fall River County, South Dakota.
27. AMNH loc. 3344. *Didymoceras nebrascense* Zone, seep, Pierre Shale, SE1/4 sec. 9, T. 9N., R. 7E. (44°45'19.9", 103°16'28.6"W), near Newell, Butte County, South Dakota.
28. AMNH loc. 3386. *Baculites scotti* Zone, seep, Pierre Shale, NW1/4 sec. 17, T. 9N., R. 7E., east of Newell, Butte County, South Dakota.
29. AMNH loc. 3440. *Didymoceras nebrascense* Zone, seep, Pierre Shale, NW1/4 sec. 10, T. 10N., R. 6E., near Newell Lake, Butte County, South Dakota.
30. AMNH loc. 3494. *Didymoceras nebrascense* Zone, seep, Pierre Shale, SE 1/4 sec. 18, T. 43N., R. 61W. (43°42'0.3"N, 104°13'55.7"W), Weston County, Wyoming.
31. AMNH loc. 3495. *Didymoceras nebrascense* Zone, seep, Pierre Shale, S1/2 sec. 7, T. 43N., R. 61W. (43°42'51.3"N, 104°13'55.7"W), Weston County, Wyoming.

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