A REVISION OF THE TURONIAN MEMBERS OF THE AMMONITE SUBFAMILY COLLIGNONICERATINAE FROM THE UNITED STATES WESTERN INTERIOR AND GULF COAST

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CONTENTS

ABSTRACT

The Collignoniceratinae of the U.S. Western Interior first appear in the lower Turonian and range through the middle, and most of the upper, Turonian. For most of their range they are important biostratigraphic indicators. A review of their biostratigraphic distribution is provided and this is followed by a revision and/or discussion of the following taxa: *Cibolaites molenaari* Cobban and Hook, 1983, *Collignoniceras woollgari woollgari* (Mantell, 1822), *C. woollgari regulare* Haas, 1946, *C. vermilionense* (Meek and Hayden, 1860), *C. jorgenseni* n. sp., *C. percarinatum* (Hall and Meek, 1856), *C. praecox* (Haas, 1946), *Collignonicerites collisniger* n. gen., n. sp., *Prionocyclus hyatti* (Stanton, 1894), *P. albinus* (Fritsch, 1872), *P. macombi* Meek, 1876, *P. bosquensis* Kennedy, 1988, *P. wyomingensis* Meek, 1876, *P. novimexicanus* (Marcou, 1858), *P. quadratus* Cobban, 1953, *P. germari* (Reuss, 1845), *P. pluricostatus* n. sp., *Prionocyclites mite* Kennedy, 1988, and *Reesidites minimus* Hayasaka and Fukada, 1951.

Collignoniceras woollgari, Prionocyclus hyatti, P. macombi, P. wyomingensis, P. novimexicanus, P. quadratus, and *P. germari* have been designated as zonal species in many publications, but aside from *C. woollgari, P. hyatti,* and *P. wyomingensis*, most of these species have not been well described in terms of their intraspecific variation. In many species, there is a gracile and a robust form, which may represent sexual dimorphs, but in most instances, the sample size of adult specimens is too small to prove this.

INTRODUCTION

The Collignoniceratidae are a family of Late Cretaceous (latest Cenomanian to middle Campanian) ammonites with a widespread distribution (North and South America, Europe, Africa, and Asia). The species are characterized by their involute to evolute coiling, generally compressed whorls, and oval to rectangular whorl section. The venter commonly bears one or several entire or serrated keels and the flanks and ventrolateral shoulders are ornamented by as many as six rows of tubercles. The Subfamily Collignoniceratinae appeared in the latest Cenomanian and persisted into the Coniacian, reaching its maximum diversity in the Turonian. Many species such as *Collignoniceras woollgari* (Mantell, 1822), *Prionocyclus hyatti* (Stanton, 1894), *P. germari* (Reuss, 1845), *P. albinus* (Fritsch, 1872), and *Cibolaites molenaari* (Cobban and Hook, 1983) are important biostratigraphic markers (Matsumoto, 1959, 1965, 1977; Wright, 1979, 1996; Amédro and Badillet, 1982; Cobban, 1984a; Kaplan, 1988; Hancock et al., 1993; Marcinowski et al., 1996).

We describe the representatives of the subfamily that occur in the Western Interior and Gulf Coast regions of the United States (fig. 1), a region where collignoniceratines are more abundant than in any other area yet described, especially in the middle and upper Turonian.

Members of the subfamily were collected and described during the early surveys of the United States Interior, notably by Marcou (1858), Hall and Meek (1856), Meek (1870, 1871, 1876a, 1876b), and Stanton (1894), while material from the Gulf Coast was described by Shumard (1860). Moreman (1927, 1942) redescribed several species from north-central Texas, but illustrated only limited material, and Adkins (1931) and Sidwell (1932) described specimens from Trans-Pecos Texas and the Western Interior, respectively. Haas (1946) provided a detailed account of variation in ''*Prionotropis*'' *woollgari* and *Prionocyclus wyomingensis* from the northern part of the Western Interior, but, unfortunately, most of his material lacked precise stratigraphic and geographic data. Powell (1963) described material from north-central Texas and Chihuahua, Mexico.

Matsumoto (1965, 1971) discussed the genera and certain species of Collignoniceratinae from North America in his revision of the Japanese members of the subfamily. Cobban (1953) described the new species *Prionocyclus quadratus* from the Interior, and reviewed other species with colleagues in subsequent publications (Cobban, 1983; Cobban et al., 1956; Cobban and Scott, 1972; Cobban and Hook, 1979, 1983; Hook and Cobban, 1979, 1980). More recently, Kennedy and Cobban (1988), Kennedy et al. (1989), and Kennedy (1988) described material from

Chihuahua, Mexico, Trans-Pecos Texas, and northeast Texas, respectively. These recent accounts, plus revisions of the type material of the European species (Kennedy et al., 1980; Wright and Kennedy, 1981; Kaplan, 1988) provide a framework in which to describe the many thousands of specimens in the collections of the U. S. Geological Survey and place these specimens in a chronostratigraphic sequence in order to establish an international faunal timescale.

LOCALITIES OF ILLUSTRATED FOSSILS

Figure 1

1. 21191. North of Belle Fourche in the N½ sec. 10, T. 9 N, R. 2 E, Butte County, South Dakota. Carlile Shale, from concretions 72–73 m (235–240 ft) above base.
2. 21192. Same locality as 21191. Carlile Shale, from concretions 73–76 m (240–250 ft) above base.
3. 21194. Same locality as 21191. Carlile Shale, from concretions 76.5–80.4 m (251–264 ft) above base.
4. 21195. North of Belle Fourche in the NW¼ sec. 10, T. 9 N, R. 2 E, Butte County, South Dakota. Carlile Shale, from concretions 83–83.5 m (272–274 ft) above base.
5. 21183. North of Belle Fourche in the SW¼ sec. 11, T. 9 N, R. 2 E, Butte County, South Dakota. Carlile Shale, from concretions 17.7–19.8 m (58–65 ft) above base.
6. 21187. Same locality as 21183. Carlile Shale, from concretions 34–35 m (111–114 ft) above base.
7. D9896. NW¼ sec. 35, T. 46 N, R. 63 W, Weston County, Wyoming. Carlile Shale, from limestone concretions 18.3 m below base of Turner Sandy Member.
8. 21792. West of Newcastle in the NW¼ sec. 31, T. 45 N, R. 61 W, Weston County, Wyoming. Carlile Shale, from limestone concretions 18.3 m (60 ft) below base of Turner Sandy Member.
9. D8849. Sec. 31, T. 37 N, R 61 W, Niobrara County, Wyoming. Carlile Shale, from middle of Turner Sandy Member.
10. D8443. Sec. 12, T. 36 N, R. 62 W, Niobrara County, Wyoming. Carlile Shale, 16 m (52.5 ft) above base of Turner Sandy Member.
11. 18872. About 3.2 km (2 mi) southeast of Fairburn, Custer County, South Dakota. Carlile Shale, from a limestone concretion in the lower part.
12. D13832. Sec. 35, T. 8 S, R. 1 E, Fall River County, South Dakota. Carlile Shale, from limestone concretions in lower part.
13. D8399. Sec. 2, T. 9 S, R. 1 E, Fall River County, South Dakota. Carlile Shale, Turner Sandy Member.
14. D13833. NW¼ SW¼ sec. 8, T. 9 S, R. 2 E, Fall River County, South Dakota. Carlile Shale, from limestone concretions in lower part of Pool Creek Member.
15. D10697. SE¼ SE¼ sec. 18, T. 9 S, R. 2 E, Fall River County, South Dakota. Carlile Shale, from limestone concretions about 6 m (20 ft) below base of Turner Sandy Member.
16. D13834. SW¼ SW¼ sec. 25, T. 7 S, R. 6 E, Fall River County, South Dakota. Carlile Shale, from a limestone concretion in lower part.
17. D13185. NE¼ SW¼ sec. 26, T. 7 S, R. 6 E, Fall River County, South Dakota. Carlile Shale, from white limestone concretions in Pool Creek Member.
18. D12215. Angostura Reservoir in the W½ sec. 34, T. 8 S, R. 6 E, Fall River County, South Dakota. Carlile Shale, from sandstone concretions 17 m above base of Turner Sandy Member.
19. D203. NE¼ NW¼ sec. 28, T. 35 N, R. 47 W, Dawes County, Nebraska. Carlile Shale, from large laminated silty limestone concretions 40–40.5 m (131–133 ft) above base.
20. D12683. Old dam site on Brule Creek in the NE¼ NW¼ sec. 32, T. 94 N, R. 50 W, Union County State Park, Union County, South Dakota. Carlile Shale.
21. D10404. Ionia Volcano in the NW¼ SE¼ sec. 3, T. 31 N, R. 5 E, Dixon County, Nebraska. Carlile Shale.
22. D1836. North Solomon River in the NE¼ sec. 27, T. 5 S, R. 13 W, Smith County, Kansas. Carlile Shale, from flat ferruginous concretions in lower part of Blue Hill Member.
23. 21838. About 4.8 km (3 mi) south-southeast of Tipton in the SE¼ sec. 4, T. 9 S, R. 10 W, Mitchell County, Kansas. Carlile Shale, from limestone concretions in upper part of Blue Hill Member.
24. D9833. NW¼ NW¼ sec. 33, T. 40 N,

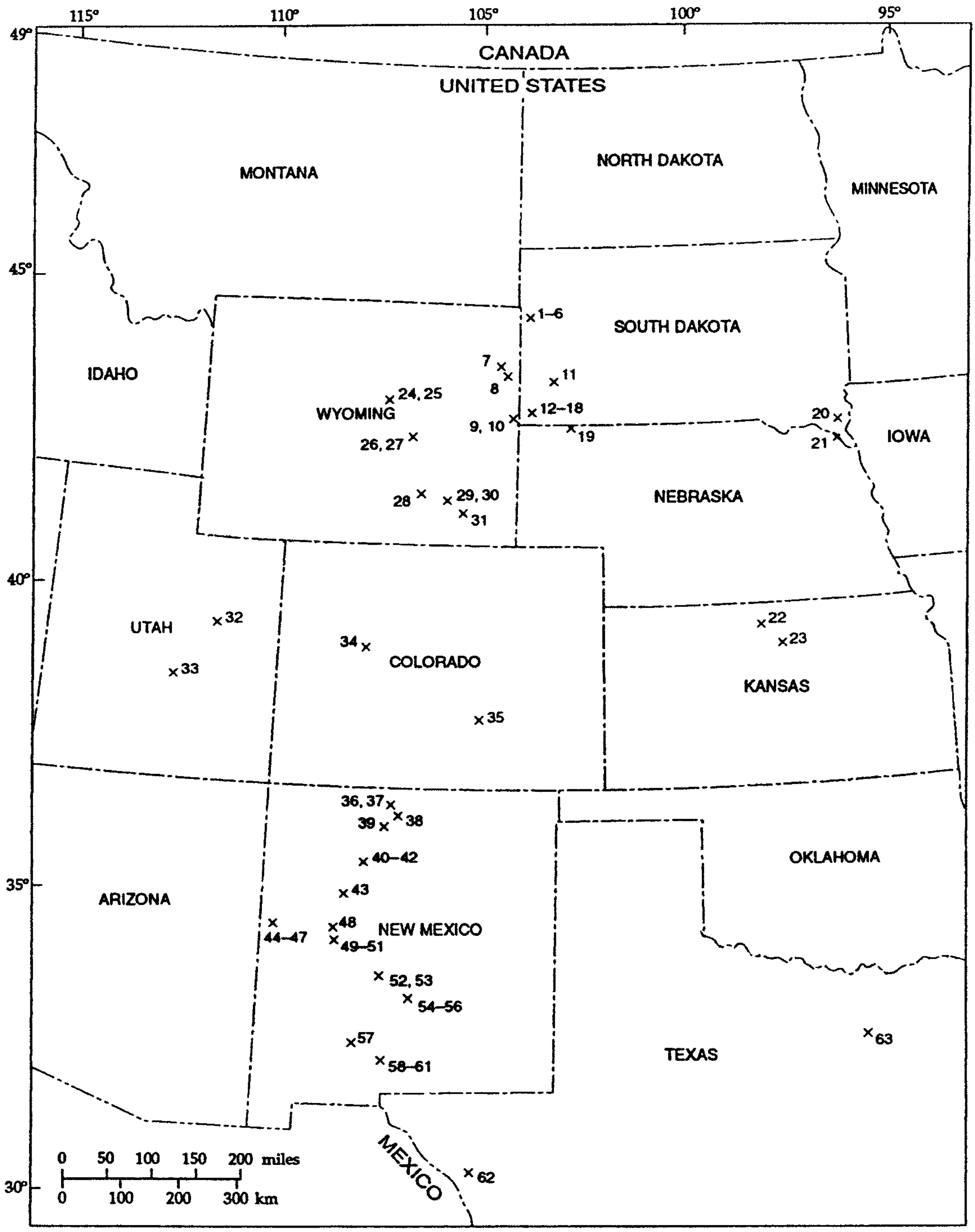

Fig. 1. Map of the U.S. Western Interior showing the localities of fossils described in the present study. See text for a description of the localities.

<table>
<tr><th>SUBSTAGE</th><th>STANDARD ZONE</th><th>COLLIGNONICERATID ZONE</th></tr>
<tr><td rowspan="3">UPPER TURONIAN</td><td>Prionocyclus germari</td><td>Prionocyclus germari</td></tr>
<tr><td>Scaphites (S.) nigricollensis</td><td rowspan="2">Prionocyclus novimexicanus</td></tr>
<tr><td>Scaphites (S.) whitfieldi</td></tr>
<tr><td rowspan="7">MIDDLE TURONIAN</td><td>Scaphites (S.) ferronensis</td><td rowspan="2">Prionocyclus wyomingensis</td></tr>
<tr><td>Scaphites (S.) warreni</td></tr>
<tr><td>Prionocyclus macombi</td><td>Prionocyclus macombi</td></tr>
<tr><td>Prionocyclus hyatti</td><td>Prionocyclus hyatti</td></tr>
<tr><td>Collignoniceras praecox</td><td>Collignoniceras praecox</td></tr>
<tr><td rowspan="2">Collignoniceras woollgari</td><td>C. w. regulare subzone</td></tr>
<tr><td>C. w. woollgari subzone</td></tr>
<tr><td rowspan="4">LOWER TURONIAN</td><td>Mammites nodosoides</td><td>level of Cibolaites</td></tr>
<tr><td>Vascoceras birchbyi</td><td rowspan="3">no collignoniceratids</td></tr>
<tr><td>Pseudaspidoceras flexuosum</td></tr>
<tr><td>Watinoceras devonense</td></tr>
</table>

Fig. 2. Turonian ammonite zonation used in the text, based on Cobban (1984a), Kennedy et al. (1989), Hancock et al. (1993), Cobban (1990), and Walaszczyk and Cobban (2000).

R. 82 W, Natrona County, Wyoming. Frontier Formation, from second ledge-forming sandstone below top.

25. D12956. At the Gap in the NE¼ NE¼ sec. 18, T. 39 N, R. 82 W, Natrona County, Wyoming. Frontier Formation, Wall Creek Member.

26. D9118. NW¼ NE¼ sec. 4, T. 33 N, R.

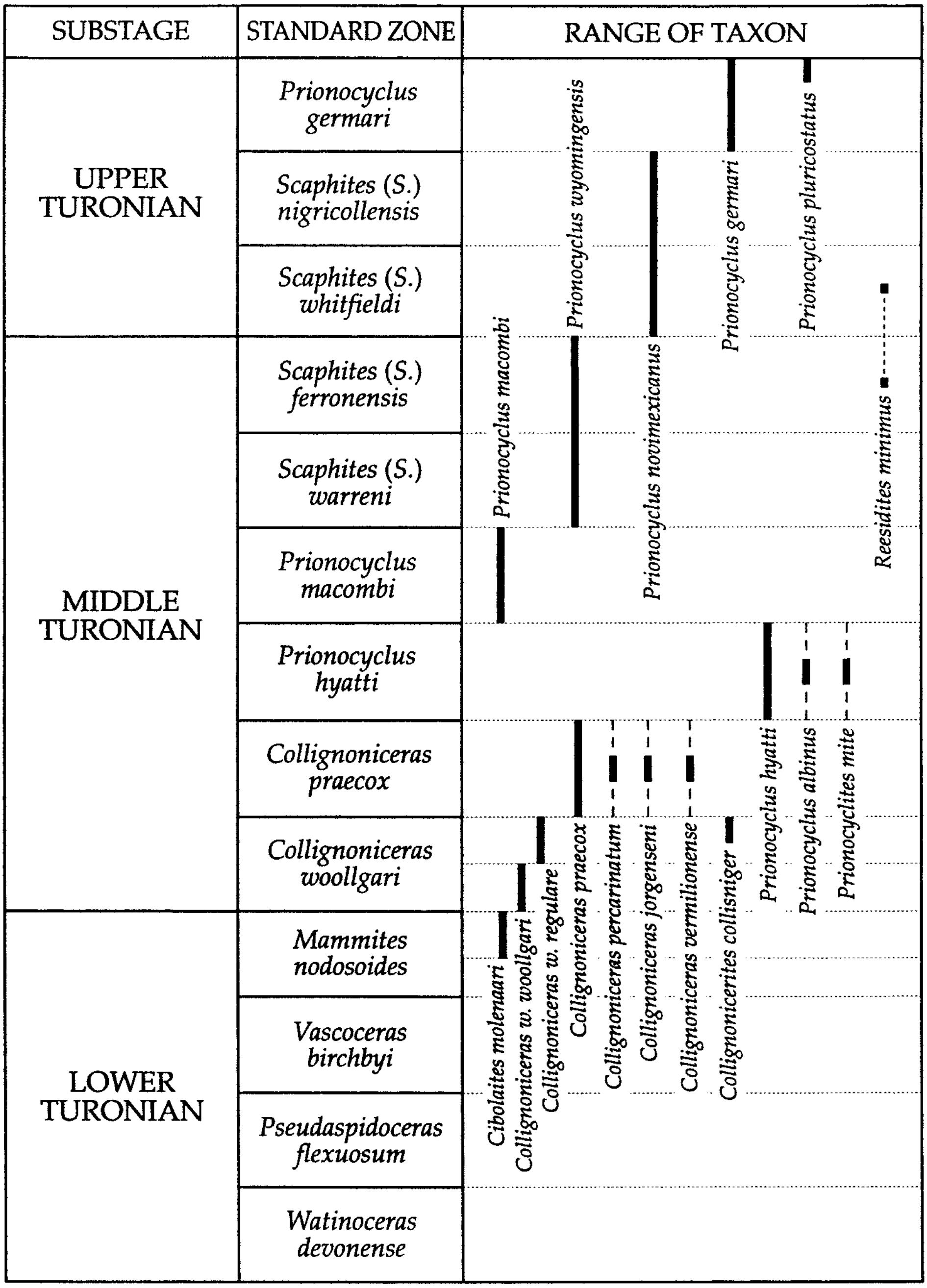

Fig. 3. Stratigraphic distribution of Collignoniceratinae in the U.S. Western Interior.

81 W, Natrona County, Wyoming. Frontier Formation, from uppermost sandstone of Wall Creek Member.

27. D9877. SE¼ NE¼ sec. 34, T. 33 N, R. 82 W, Natrona County, Wyoming. Frontier Formation, from small limestone concretions 7–9 m above a sandstone unit bearing *Collignoniceras woollgari.*

28. D3763. About 2 km north of Medicine Bow in center of the SE¼ sec. 32, T. 23 N,

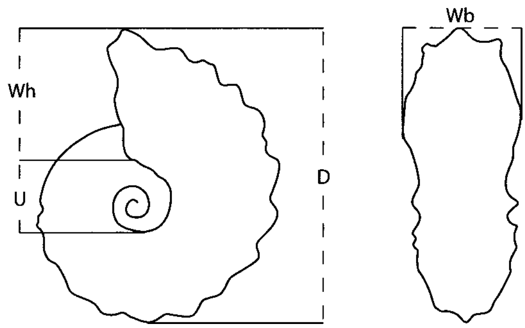

Fig. 4. Measurements used in the text: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter.

R. 78 W, Carbon County, Wyoming. Frontier Formation, from basal ledges of Wall Creek Member.

29. D9244. NE¼ sec. 7, T. 21 N, R. 74 W, Albany County, Wyoming. Frontier Formation, from lowest ledge-forming sandstone bed of Wall Creek Member.

30. D6928. NE¼ SW¼ sec. 31, T. 22 N, R. 75 W, Albany County, Wyoming. Frontier Formation, Wall Creek Sandstone Member.

31. D8981. SE¼ NW¼ sec. 25, T. 19 N, R. 71 W, Albany County, Wyoming. Frontier Formation, from uppermost part of Wall Creek Sandstone Member.

32. 23422. SE¼ sec. 15, T. 15 S, R. 12 E, Carbon County, Utah. Mancos Shale, from silty, septarian, limestone concretions below the Ferron Sandstone Member.

33. D7227. About 8 km east of Ferron, in the NW¼ sec. 9, T. 20 S, R. 8 E, Emery County, Utah. Mancos Shale, about 30 m (98 ft) above Ferron Sandstone Member.

34. D11898. NW¼ SE¼ sec. 22, T. 8 S, R. 87 W, Pitkin County, Colorado. Mancos Shale, from calcareous shale 4 m (13 ft) below base of Fort Hays Limestone Member.

35. D3993. NW¼ sec. 20, T. 20 S, R. 65 W, Pueblo County, Colorado. Carlile Shale, from concretion in Blue Hill Member.

36. 17632. North of El Vado, Rio Arriba County, New Mexico. Mancos Shale, Juana Lopez Member.

37. D2895. About 14 km south of Chama, Rio Arriba County, New Mexico. Mancos Shale, Juana Lopez Member.

38. D4407. NW¼ sec. 25, T. 26 N, R. 4 E, Rio Arriba County, New Mexico. Mancos Shale, Juana Lopez Member.

39. D4395. North of Rio Gallina in SE¼ sec. 15, T. 25 N, R. 1 E, Rio Arriba County, New Mexico. Mancos Shale, from base of Juana Lopez Member.

40. D3884. Arroyo Lopez 1 km north of Holy Ghost Spring, Sandoval County, New Mexico. Mancos Shale, from basal part of Semilla Sandstone Member (for map, see Dane et al., 1968).

41. 28873. Arroyo Lopez 0.6–0.9 km north of Holy Ghost Spring, Sandoval County, New Mexico. Mancos Shale, from basal part of Semilla Sandstone Member.

42. D3694. About 13.3 km (8.3 mi) south of La Ventana, Sandoval County, New Mexico. Mancos Shale, from basal part of Semilla Sandstone Member.

43. D5349. About 3.2 km (2 mi) east of Seboyeta, Cibola County, New Mexico. Mancos Shale, from a limestone concretion 18 m (60 ft) above top of main ledge of Juana Lopez Member.

44. D11208. NE¼ sec. 36, T. 6 N, R. 19 W, Cibola County, New Mexico. Mancos Shale, D-Cross Member.

45. D11281. NE¼ sec. 2, T. 5 N, R. 20 W, Cibola County, New Mexico. Same stratigraphic position as D8429.

46. D11342. NE¼ sec. 2, T. 5 N, R. 19 W, Cibola County, New Mexico. Mancos Shale, near top.

47. D8429. Sec. 1 and NE¼ sec. 12, T. 4 N, R. 19 W, Cibola County, New Mexico. Mancos Shale, from limestone concretions 24–30 m (78–97 ft) below top of Rio Salado Tongue.

48. D10525. W½ NW¼ sec. 10, T. 4 N, R. 7 W, Cibola County, New Mexico. Mancos

Fig. 5. *Cibolaites molenaari* Cobban and Hook, 1983. Holotype, USNM 328766, a gracile individual from locality 44. All figures are ×1.

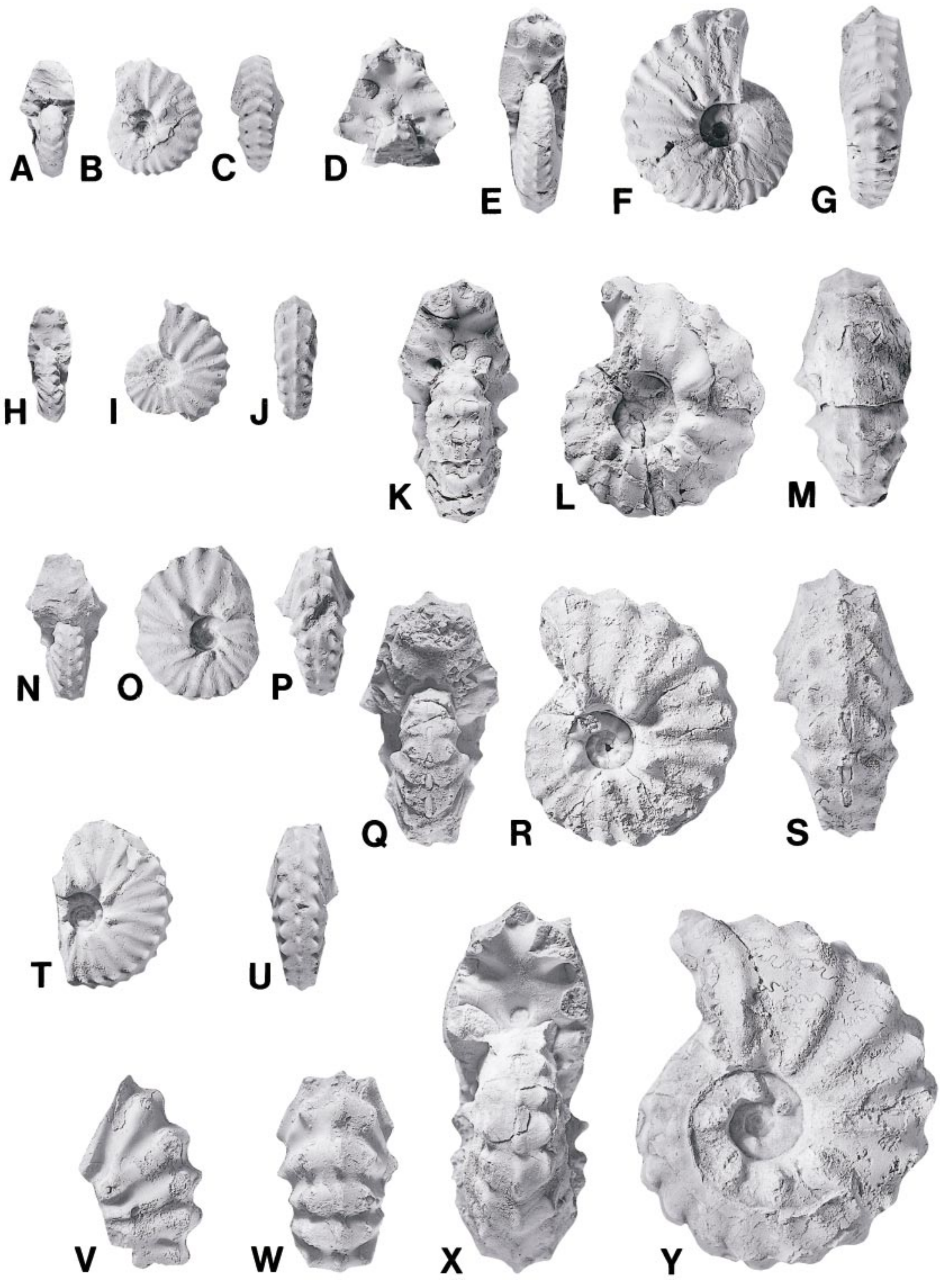

Fig. 6. *Cibolaites molenaari* Cobban and Hook, 1983. **A–C**. Paratype USNM 328761, a gracile

TABLE 1
Dimensions (mm) of *Cibolaites molenaari* Cobban and Hook, 1983[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
USNM 489202	Costal	42.1 (100)	23.9 (56.8)	19.7 (46.8)	1.21	9.3 (22.1)
	Intercostal	39.0 (100)	17.0 (43.6)	17.4 (44.6)	0.98	9.3 (23.8)
USNM 489203	Costal	42.1 (100)	24.1 (57.2)	18.9 (44.8)	1.28	9.5 (22.6)
	Intercostal	38.4 (100)	18.0 (46.9)	17.0 (44.3)	1.06	9.5 (24.7)
USNM 489204	Costal	64.2 (100)	26.0 (40.5)	25.1 (39.0)	1.04	15.9 (24.8)
	Intercostal	57.0 (100)	21.7 (38.0)	24.3 (42.6)	0.89	15.9 (27.9)
USNM 489205	Costal	64.8 (100)	25.2 (38.9)	31.4 (48.4)	0.80	13.0 (20.1)
	Intercostal	59.3 (100)	24.4 (41.1)	28.9 (48.7)	0.84	13.0 (21.9)
USNM 489206	Costal	72.6 (100)	35.6 (49.0)	34.7 (47.8)	1.03	15.0 (20.7)
	Intercostal	69.7 (100)	30.3 (43.5)	32.6 (46.8)	0.93	15.0 (21.5)
USNM 489207	Costal	73.3 (100)	32.8 (44.7)	32.2 (43.9)	1.02	17.5 (23.9)
	Intercostal	66.0 (100)	29.5 (44.7)	28.7 (43.5)	1.03	17.5 (26.5)
USNM 489208	Costal	84.3 (100)	33.5 (39.7)	40.3 (47.8)	0.83	23.0 (27.3)
	Intercostal	82.0 (100)	32.0 (39.0)	36.6 (44.6)	0.87	23.0 (28.0)
USNM 489209	Costal	92.5 (100)	37.2 (40.2)	44.0 (47.6)	0.84	20.5 (22.1)
	Intercostal	88.0 (100)	33.2 (37.7)	42.5 (48.3)	0.78	20.5 (23.3)
USNM 489210	Costal	94.5 (100)	37.3 (39.5)	38.0 (40.2)	0.98	28.4 (30.1)
	Intercostal	91.4 (100)	33.9 (37.1)	36.5 (39.9)	0.93	28.4 (31.1)
USNM 489211	Costal	118.0 (100)	35.5 (30.1)	48.5 (41.1)	0.73	34.1 (28.9)
	Intercostal	116.5 (100)	34.7 (29.8)	48.0 (41.2)	0.72	34.1 (29.3)

[a] D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilical diameter. Figures in parentheses are dimensions as a percentage of diameter.

Shale, from septarian limestone concretions in Rio Salado Tongue.

49. D5773. NW¼ NW¼ sec. 24, T. 3 N, R. 7 W, Socorro County, New Mexico. Mancos Shale, from Rio Salado Tongue.

50. D10297. NW¼ NW¼ sec. 29, T. 3 N, R. 8 W, Socorro County, New Mexico. Top of Rio Salado Tongue of Mancos Shale (Hook et al., 1983: sheet 1).

51. D10127. N½ sec. 7, T. 2 N, R. 5 W, Socorro County, New Mexico. Mancos Shale, from a little above Juana Lopez Member.

52. D10240. SE¼ SE¼ sec. 8, T. 5 S, R. 2 E, Socorro County, New Mexico. Rio Salado Tongue of Mancos Shale.

53. D10243. E½ NE¼ sec. 9, T. 5 S, R. 2 E, Socorro County, New Mexico. Mancos Shale, from Rio Salado Tongue.

54. D10643. SE¼ SW¼ sec. 24, T. 9 S, R. 8 E, Lincoln County, New Mexico. Mancos Shale, from sandy limestone concretions in Rio Salado Tongue.

55. D10644. SW¼ SE¼ sec. 24, T. 9 S, R. 8 E, Lincoln County, New Mexico. Mancos Shale, from sandstone concretion 9 m (30 ft) above base of D-Cross Tongue.

56. D10636. NE¼ NE¼ sec. 25, T. 9 S, R. 8 E, Lincoln County, New Mexico. D-Cross Tongue of Mancos Shale, from sandstone concretions 9 m (29.5 ft) above base.

57. D10120. East side of Mescal Canyon about 1 km above mouth, Sierra County, New Mexico. D-Cross Tongue of Mancos Shale.

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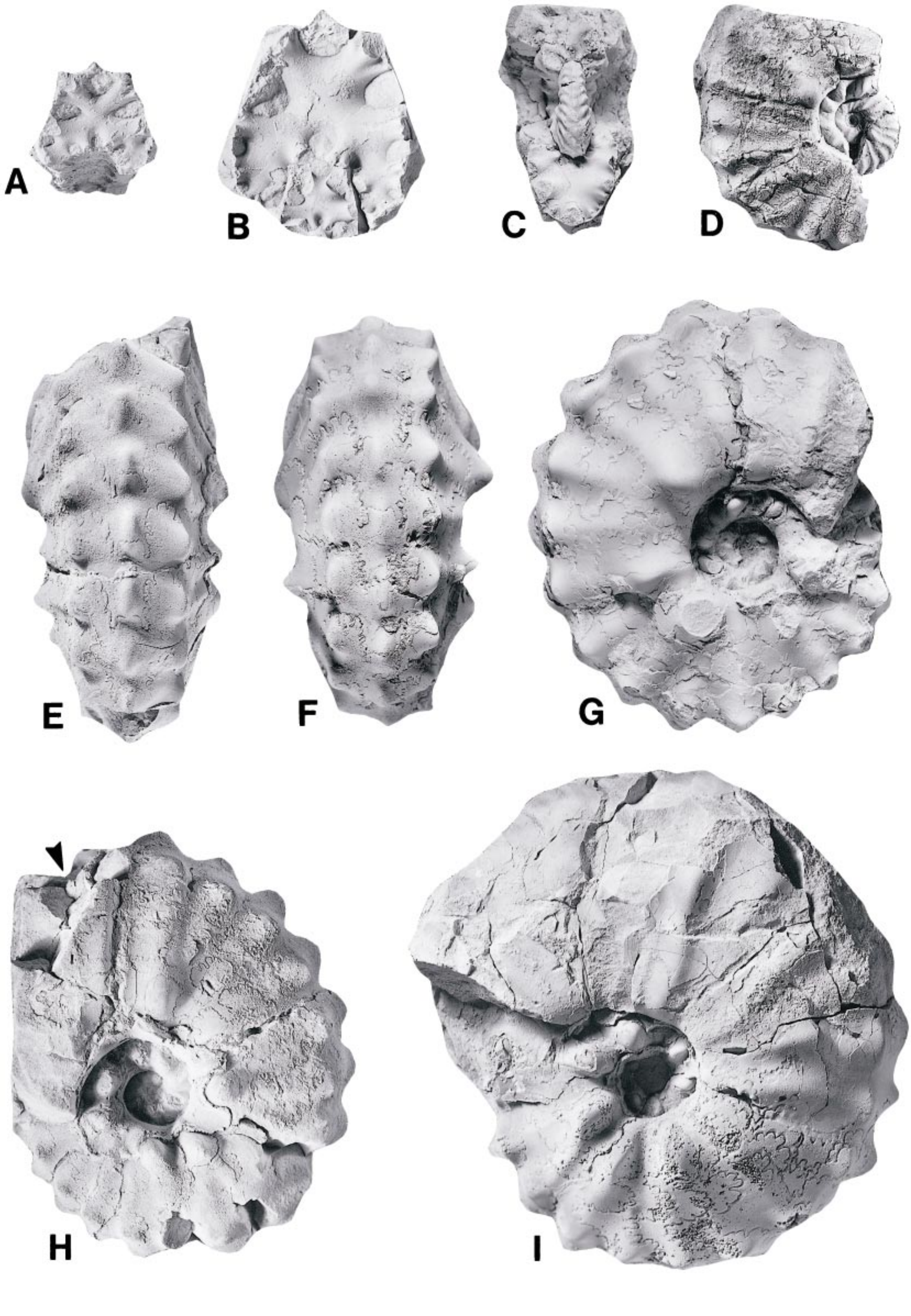
individual from locality 46. **D**. Paratype USNM 328765, a robust individual from locality 47. **E–G**. Paratype USNM 328757, a gracile individual from locality 45. **H–J**. Paratype USNM 328762, a gracile individual from locality 47. **K–M**. USNM 498202, a robust individual from locality 45. **N–P**. USNM 328763, a gracile form from locality 47. **Q–S**. USNM 498203, a robust form from locality 44. **T, U**. Paratype USNM 328755, a gracile form from locality 47. **V, W**. USNM 498212, a robust form from locality 47. **X, Y**. USNM 498205, a robust form from locality 47. All figures are ×1.


A
B
C
D
E
F
G
H
I

58. D2495. SW¼ sec. 19, T. 20 S, R. 4 E, Doña Ana County, New Mexico. Mancos Shale, from concretions in D-Cross Member.

59. D12671. North of Davis Well in the NW¼ NW¼ sec. 19, T. 20 S, R. 4 E, Doña Ana County, New Mexico. Mancos Shale, from limestone concretions in D-Cross Tongue.

60. D2494. SW¼ sec. 19, T. 20 S, R. 4 E, Doña Ana County, New Mexico. Mancos Shale, from concretions in D-Cross Member.

61. D12672. SW¼ sec. 30, T. 20 S, R. 4 E, Doña Ana County, New Mexico. D-Cross Tongue of Mancos Shale.

62. D11186. One km N 87°E of Needle Peak, Jeff Davis County, Texas. Chispa Summit Formation.

63. 22608. White Rock Scarp 3.2 km west of Cedar Hill, Dallas County, Texas. Arcadia Park Formation, 23 m (75 ft) below top.

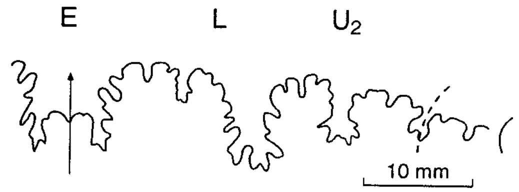


Fig. 8. *Cibolaites molenaari* Cobban and Hook, 1983. External suture line of USNM 328760 from locality 44. From Cobban and Hook (1983, fig. 14C).

BIOSTRATIGRAPHIC DISTRIBUTION OF THE COLLIGNONICERATINAE

The ammonite zones recognized here are shown in Figure 2, and are based on the work of Cobban (1984a), Kennedy et al. (1989), Hancock et al. (1993), Cobban (1990), and Walaszczyk and Cobban (2000), where detailed supporting arguments for the succession are set out.

In recent years, the Turonian Stage has been informally subdivided into lower, middle, and upper Turonian substages. During the 1995 Second International Symposium on Cretaceous Stage Boundaries in Brussels (Rawson et al., 1996), the base of the lower Turonian was placed at the first occurrence of the ammonite *Watinoceras devonense,* and the base of the middle Turonian was placed at the lowest occurrence of the ammonite *Collignoniceras woollgari* (see Bengston, 1996). No proposal was set forth for the base of the upper Turonian.

Turonian rocks in the Western Interior region were first assigned to lower, middle, and upper Turonian by Kauffman et al. (1978). They regarded the highest occurrence of the ammonite *Sciponoceras gracile* as the base of the Turonian, and the appearance of *Collignoniceras* and *Prionocyclus* as the base of the middle Turonian. A regional disconformity marked the base of rocks assigned to the upper Turonian. The base of the upper Turonian was more formally placed at the first appearance of the ammonite *Prionocyclus macombi* by Cobban and Hook (1979), but Walaszczyk and Cobban (2000) have recently shown that it occurs at a higher position (base of *Scaphites whitfieldi* Zone).

Figure 3 summarizes the biostratigraphic range distribution of the subfamily in the U.S. Western Interior. The earliest collignoniceratine is *Cibolaites* Cobban and Hook, 1983, with type and only described species *Cibolaites molenaari* Cobban and Hook, 1983 (p. 16, pl. 2, figs. 1–9; pl. 3, figs. 3–8; pl. 8, figs. 6–8; pl. 13, figs. 1–6; text-figs. 13, 14). This was originally described from the upper lower Turonian *Mammites nodosoides* Zone of New Mexico, but the genus has subsequently been reported (as *C.* cf. *molenaari*) from the upper Cenomanian *Neocardioceras juddii* Zone of Aube, France (Kennedy et al., 1986: 209, fig. 5i, j, k, l) and the lower Turonian of Germany (Kaplan, 1988).

Collignoniceras? sp. of Wright and Kennedy (1981: 107, pl. 8, fig. 17) from the upper Cenomanian of Devon, England, also ap-

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Fig. 7. *Cibolaites molenaari* Cobban and Hook, 1983. **A**. USNM 498212; **B**. USNM 498213, both robust forms from locality 47. **C, D**. USNM 498214; **E, H**. USNM 498206; **F, G**. USNM 356901; **I**. USNM 498207, all robust forms from locality 44. All figures are ×1.

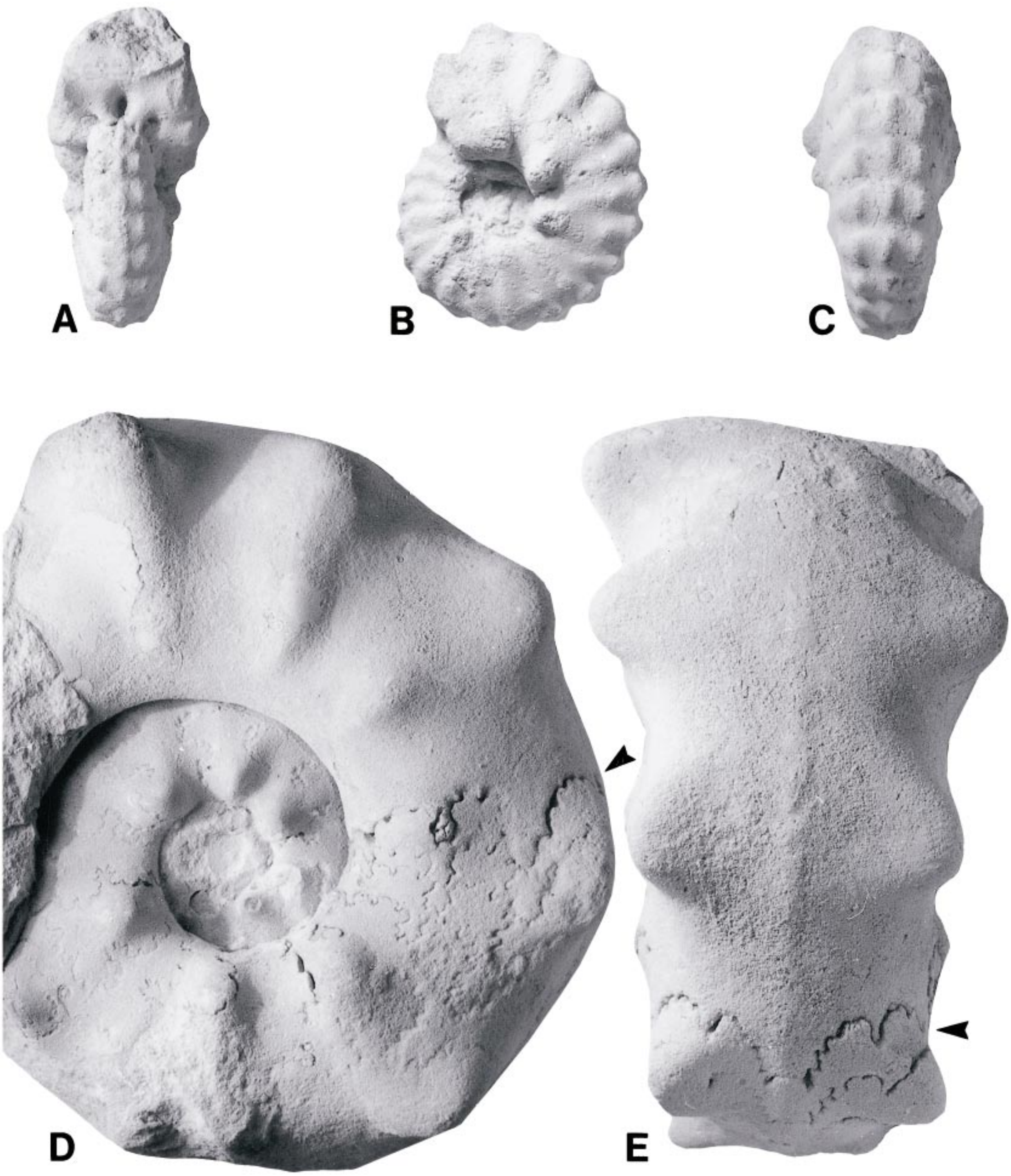
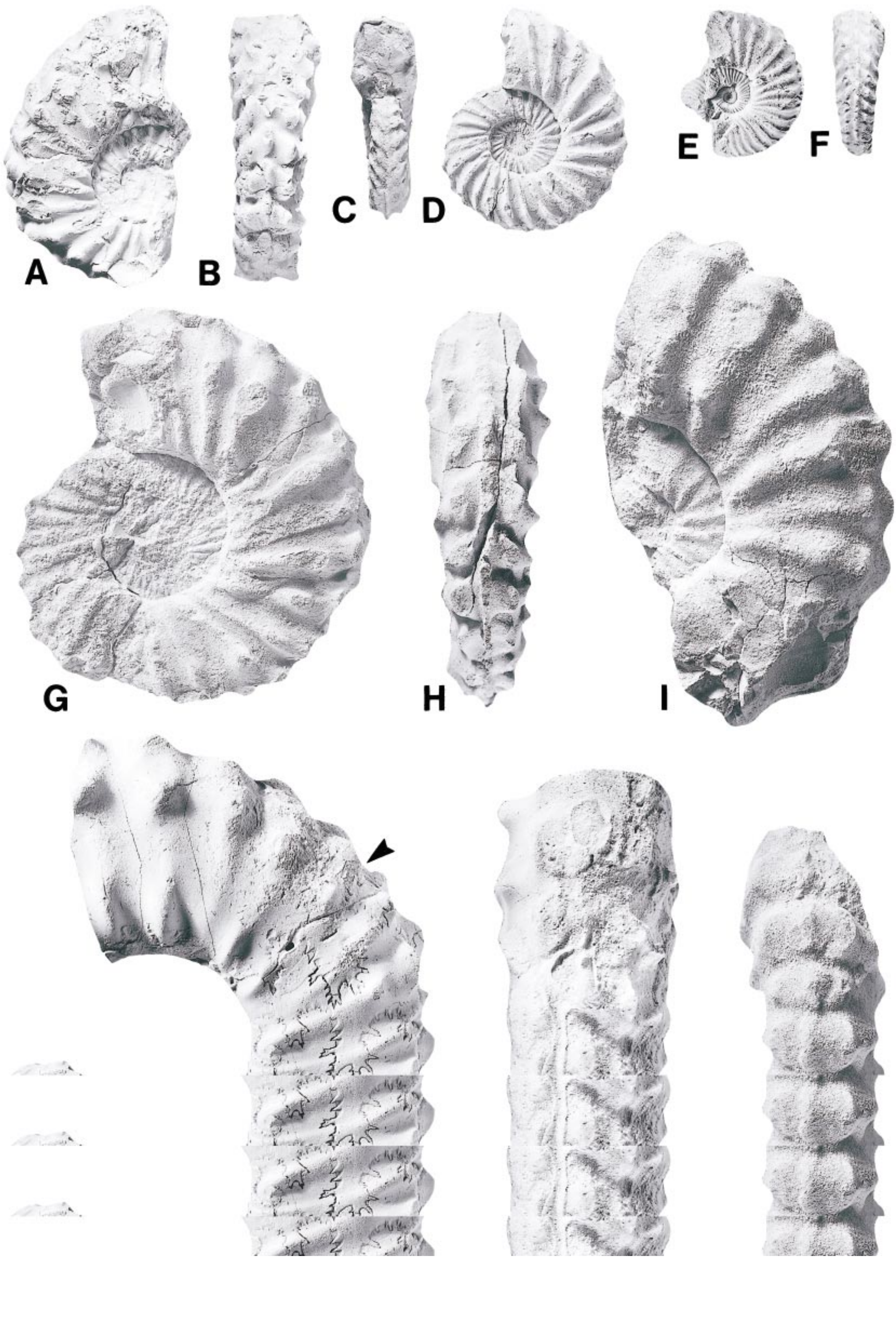


Fig. 9. *Lecointriceras fleuriausianum* (d'Orbigny, 1841). **A–C**. No. 629b in the Collections of the Château de Saumur, from the lower middle Turonian in the environs of Saumur, Maine-et-Loire, France. **D, E**. No. 122 in the Collections of the Faculté des Sciences, Le Mans, from the same horizon in Sarthe, France. All figures are ×1.

Fig. 10. *Collignoniceras woollgari woollgari* (Mantell, 1822). The lectotype BMNH 5682, the original of Mantell, 1822: plate 21, figure 6, from near Lewes, Sussex, England. Figures are ×1.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pears to be a *Cibolaites*. The distinctive features of the genus are the presence, during most of ontogeny, of umbilical, ventrolateral, and siphonal tubercles. It differs from most contemporaneous Acanthoceratinae in that it only has a single row of ventrolateral tubercles. Apart from this difference, the gross shell form of certain *Thomelites* Wright and Kennedy, 1973 (*in* Juignet et al., 1973) is similar to *Cibolaites* (Wright and Kennedy, 1990: 285, pls. 80–84).

Cibolaites is succeeded stratigraphically in Europe by *Lecointriceras* Kennedy et al., 1980 (type species *Lecointriceras fleuriausianum* (D'Orbigny, 1841) (p. 350, pl. 107, figs. 1–3)), a genus widespread in Touraine and Aquitaine in France but also recorded from northern Spain, the Czech Republic, north Germany, and southern England. The genus is middle Turonian, but later observations by Kennedy in the area around Cizay-la-Madelaine, southeast of Saumur in Touraine, France (see Kennedy and Juignet, 1981: figs. 1, 2) suggest it may extend down into the top of the lower Turonian *Mammites nodosoides* Zone. Inner whorls of *Lecointriceras* are characterized by umbilical, feeble or no inner ventrolateral, and strong outer ventrolateral and siphonal tubercles (see Kennedy et al., 1980: pl. 74, figs. 3–10), features similar to those of *Cibolaites*. However, the body chamber characters readily distinguish the two genera. In *Cibolaites*, the mature body chamber is flat-sided with progressively weakening tubercles and ribs. In *Lecointriceras*, the ribs and tubercles strengthen with the development of massive ventrolateral horns, a flattened venter, and tubular, near-smooth terminal portion immediately prior to the adult aperture; adults of the type species are dimorphic (Kennedy et al., 1984). *Lecointriceras* thus preserves in its earliest ontogeny features similar to those of *Cibolaites*, but by its development of inner ventrolateral or outer lateral tubercles as well as a distinctive body chamber ornament, it more closely resembles the morphology of stratigraphically younger *Collignoniceras* species.

Collignoniceras ranges through the *woollgari* Zone and into the *neptuni* Zone in Europe (Kennedy et al., 1986); in the U.S. Western Interior it disappears somewhat earlier, prior to the *Prionocyclus hyatti* Zone. The type species, *C. woollgari* (Mantell, 1822), occurs in both regions as well as in Turkmenistan, Japan, California, Oregon, and northern Australia. Species of the genus are dimorphic (Kennedy et al., 1989), with differences in size and ornament.

Collignoniceras woollgari can be distinguished from *Lecointriceras* in that the latter has a trapezoidal whorl section, and sparse low ribs in early growth, with blunt ventrolateral horns on the adult body chamber. *Collignoniceras woollgari* is compressed and finely ribbed in early and middle growth, with siphonal clavi maintained to maturity. Very small specimens (up to 7 mm diameter) of *C. woollgari* have trituberculate venters (Cobban and Hook, 1979: pl. 2, figs. 18, 19). At maturity, ribbing coarsens markedly in both dimorphs of *C. woollgari*, with large umbilical flares, large ventrolateral horns and a final, nearly smooth, tubular portion of the adult body chamber, a general style of ornament similar to adult *Lecointriceras*, but with the addition of persistent siphonal clavi.

Merewether et al. (1979) drew attention to the occurrence of both early and late forms of *C. woollgari* in the U.S. Western Interior, an observation expanded on by Cobban and Hook (1979), who recognized an earlier *C. woollgari woollgari* and a later *C. woollgari regulare* (which are taken as indices of two subzones of the *woollgari* Zone; fig. 2). They differ in that *C. woollgari woollgari* has middle and late growth stages characterized by secondary ribs, more siphonal tubercles than ventrolateral ones, and looped ribs connect-

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Fig. 11. *Collignoniceras woollgari woollgari* (Mantell, 1822). **A, B**. USNM 420009, a gracile form from locality 62. **C, D**. USNM 252793, a gracile form from locality 50. **E, F**. USNM 252795, a gracile form from locality 52. **G, H**. USNM 356903, a gracile form from locality 53. **I, J**. USNM 498215, a gracile form from locality 49. **K, L**. USNM 420010, a gracile form from locality 62. All figures are ×1.

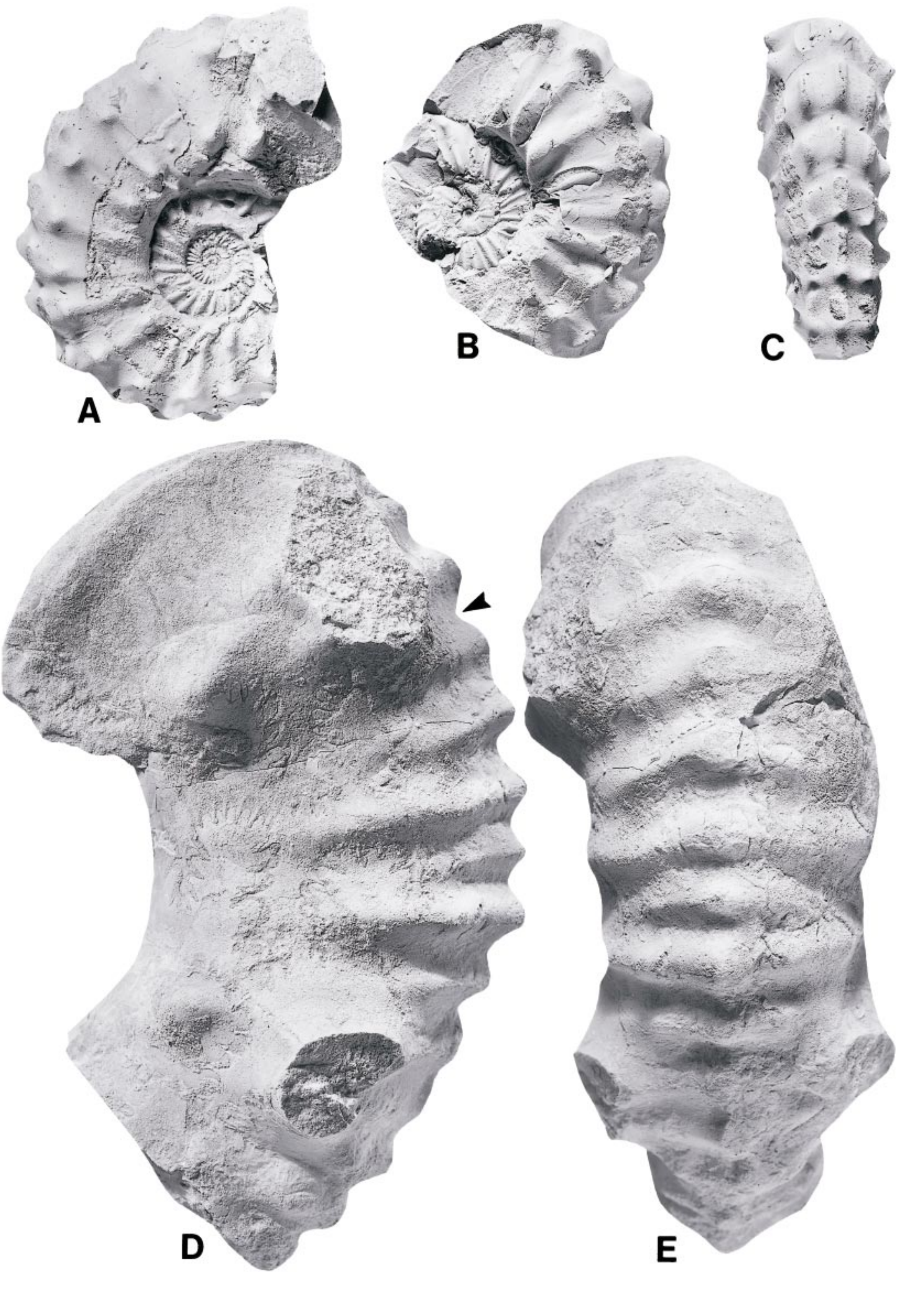
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Fig. 13. *Collignoniceras woollgari woollgari* (Mantell, 1822). USNM 498216, from locality 48. Figure is ×1.

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Fig. 12. *Collignoniceras woollgari woollgari* (Mantell, 1822). **A**. USNM 420006; **B, C**. USNM 420007, both gracile forms from locality 62. **D, E**. USNM 403228, a robust form from locality 54. All figures are ×1.

Fig. 14. *Collignoniceras woollgari woollgari* (Mantell, 1822). USNM 498216, from locality 48. Figure is ×1.

ing ventrolateral horns, whereas *C. woollgari regulare* lacks these features in middle growth. Adult body chambers of the two subspecies may, however, be inseparable in some cases. Kennedy et al. (1986) recorded fragments with intercalated ribs from the upper Turonian of Aube, France, but these are bits of body chamber, and restudy of material from Touraine in France shows that the two successive subspecies can also be recognized there, and indeed elsewhere in western Europe.

There are several other species of *Collignoniceras* that co-occur with *Collignoniceras woollgari* in western Europe. *Collignoniceras carolinum* (D'Orbigny, 1850) (p. 310, pl. 9, figs. 5, 6; Kennedy et al., 1980: 574, pl. 68, figs. 1–11; pl. 76, figs. 1, 2; text-figs. 1B, 5) is a small species (up to 12 cm adult diameter) that is finely and densely ribbed and does not develop hypernodose body chamber ornament; it ranges through much of the European *woollgari* Zone. *Collignoniceras papale* (D'Orbigny, 1841) (p. 354, pl. 109, figs. 1–3; Kennedy et al., 1980: 578, pl. 69, figs. 1, 2; pl. 70, figs. 3–5; text-figs. 1c, 6, 7), is a coarsely ribbed, medium-sized species (up to 17 cm adult diameter) of the *regulare* Subzone that also lacks hypernodose body cham-

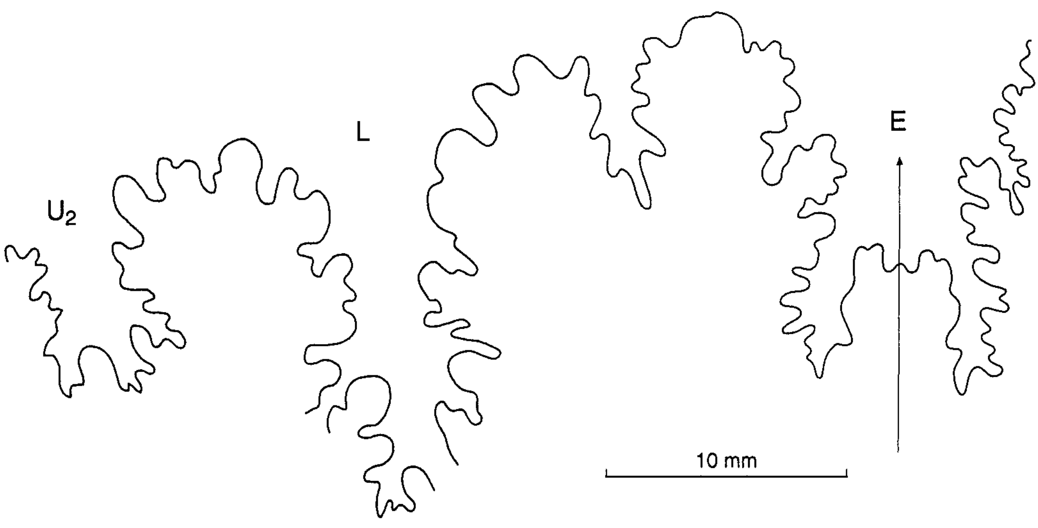

Fig. 15. External suture of *Collignoniceras woollgari woollgari* (Mantell, 1822), taken from Oxford University Museum of Natural History Collections, no. KT 1275, Ojinaga Formation, middle Turonian, *C. woollgari* Zone, *C. woollgari woollgari* Subzone, Cannonball Hill, Chihuahua, Mexico.

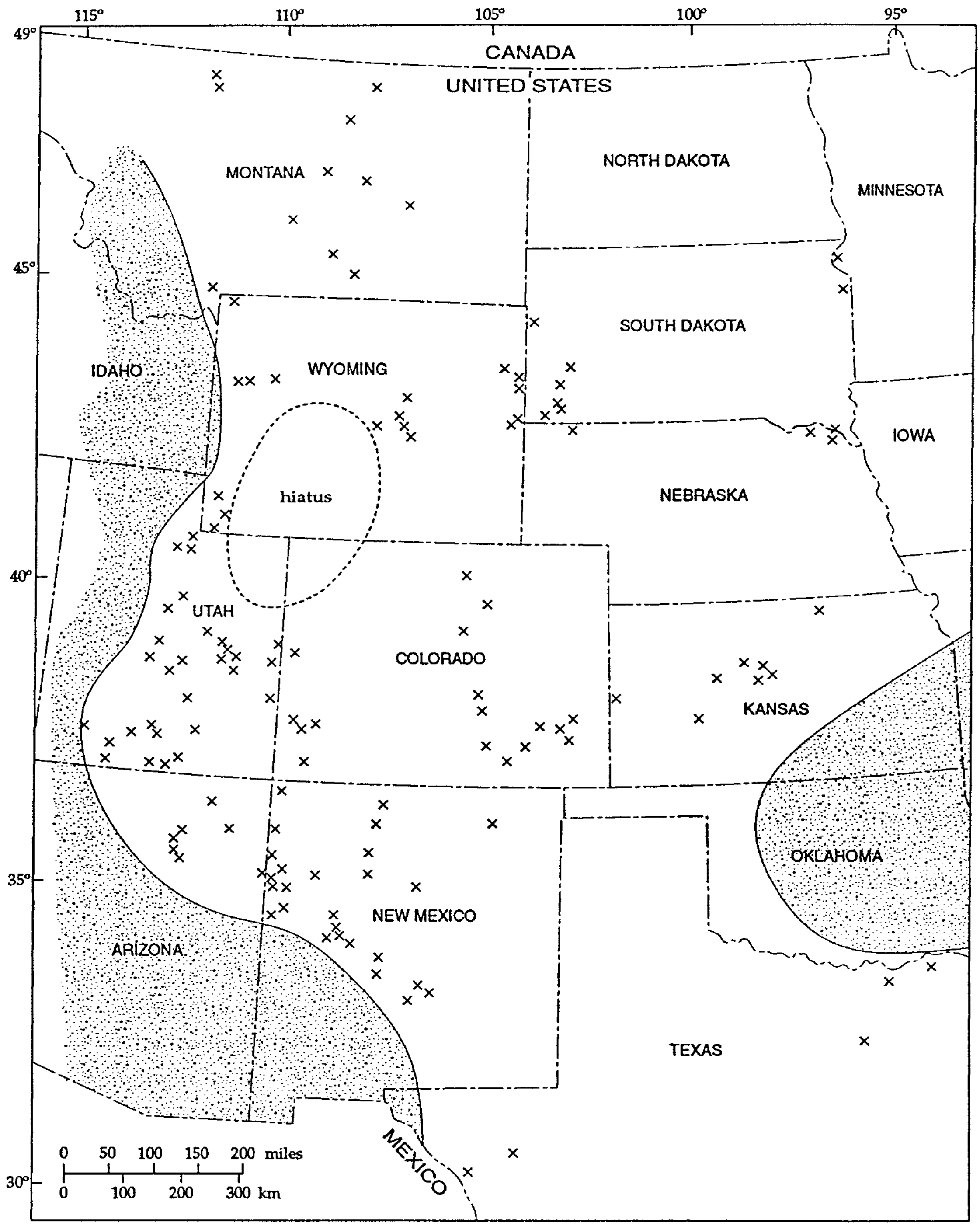

Fig. 16. Distribution of *Collignoniceras woollgari woollgari* (Mantell, 1822), and *C. woollgari regulare* (Haas, 1946) in the Western Interior Seaway during the early middle Turonian. Land areas indicated by stipple. Modified after Cobban et al., 1994.

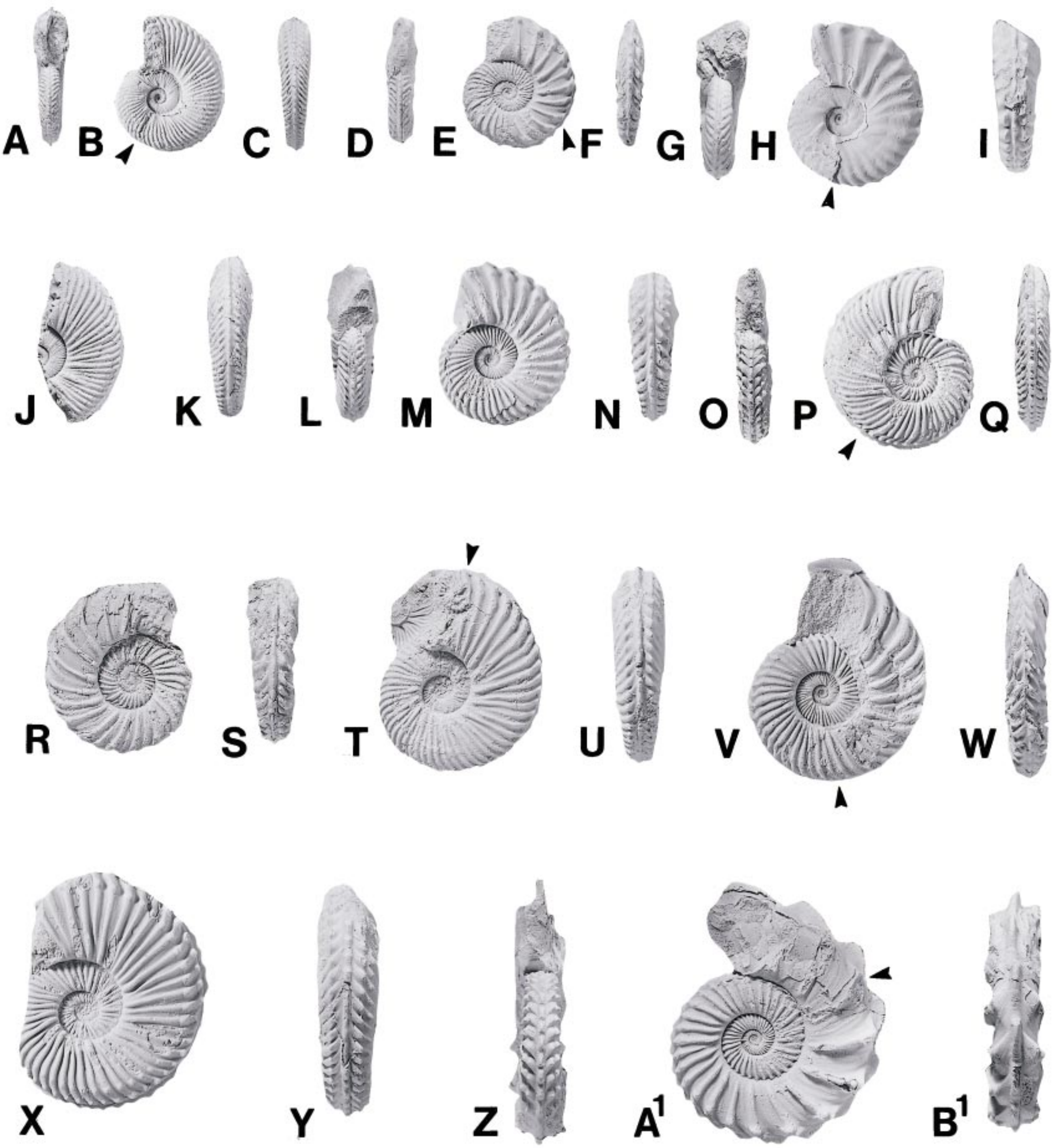

Fig. 17. *Collignoniceras woollgari regulare* (Haas, 1946), gracile form. **A–C**. USNM 498227; **D–F**. USNM 498217; **G–I**. USNM 498228; **J, K**. USNM 498229; **L–N**. USNM 498221; **O–Q**. USNM 498230; **R, S**. USNM 498231, all from locality 8. **T, U**. USNM 498232, from locality 12. **V, W**. USNM 498233, from locality 8. **X, Y**. USNM 498234, from locality 12. **Z–B^1**. USNM 498223, from locality 8. All figures are ×1.

ber ornament and is dimorphic (Kennedy et al., 1984). *Collignoniceras canthus* (Sornay, 1951) (p. 629, text-figs. 1, 2; Kennedy et al., 1980: 582, pl. 73, figs. 1–4) is a rare, medium-sized species with coarsely ornamented inner whorls but a weakly ornamented body chamber. *Collignoniceras turoniense* (Sornay, 1951) (p. 630, pl. 21, figs. 1–3; Kennedy

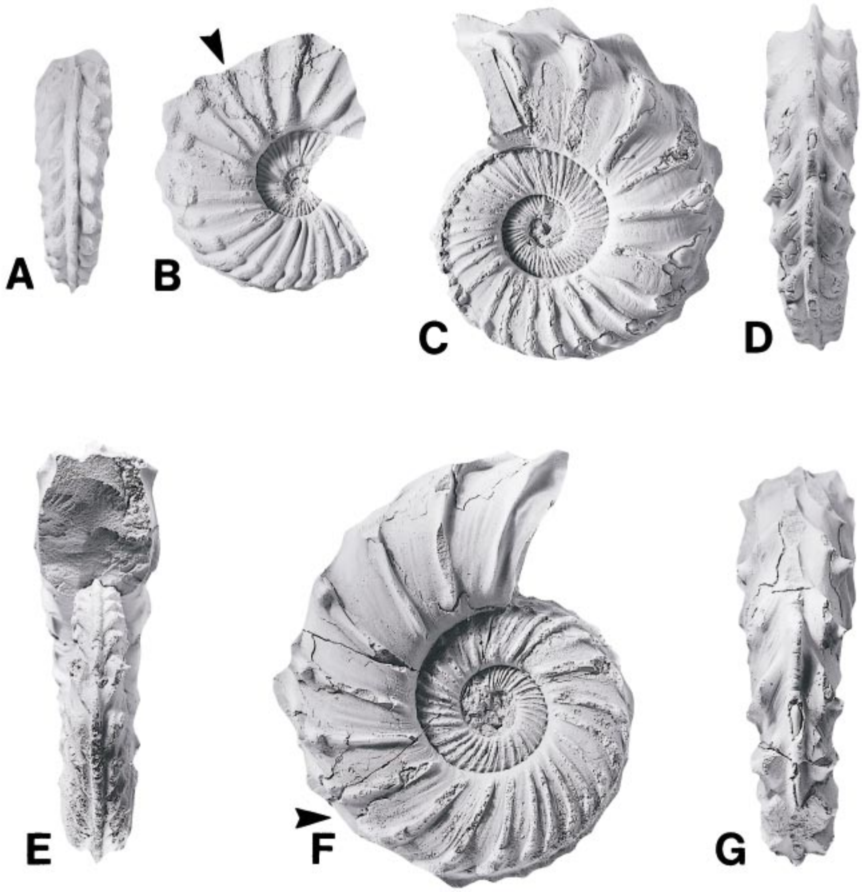

Fig. 18. *Collignoniceras woollgari regulare* (Haas, 1946), gracile form. **A, B**. USNM 498235, from locality 12. **C, D**. USNM 498236; **E–G**. USNM 498237, both from locality 8. All figures are ×1.

et al., 1980: 584, pl. 71, figs. 4, 5; pl. 72, figs. 1–3) is a medium-sized species with coarse ornament throughout.

In the U.S. Western Interior, *C. woollgari* disappears earlier in the middle Turonian than in western Europe, and is replaced by four endemic species: *Collignoniceras vermilionense* (Meek and Hayden, 1860), *C. jorgenseni* n. sp., *C. percarinatum* (Hall and Meek, 1856), and *C. praecox* (Haas, 1946). *Collignoniceras vermilionense* is a diminutive, very evolute species, with ribs that lack well-defined ventrolateral tubercles. It is smaller than *C. woollgari regulare*. *Collignoniceras praecox* differs from *C. woollgari regulare* by the persistence of long and short ribs, with ventrolateral tubercles outnumbering the umbilical ones, and a nearly continuous siphonal keel, whereas in *C. woollgari regulare* the number of siphonal clavi equals the number of ventrolateral tubercles except in occasional, very large individuals (30 cm diameter). These features also separate *C. praecox* from *C. vermilionense*, as does the retention of inner and outer ventrolateral tubercles in *C. praecox* at an ontogenetic stage when they are absent in *C. vermilionense*. *Collignoniceras jorgenseni* is a small species with prorsiradiate primary and secondary ribs throughout ontogeny, bullate primary ribs, inner and outer ventrolateral tubercles, siphonal clavi equal in number to the ribs, and primary ribs that are commonly flared.

In the middle Turonian Western Interior,

Fig. 19. *Collignoniceras woollgari regulare* (Haas, 1946), gracile form. USNM 498238, from locality 17. Figure is ×1.

there are two diminutive species that are presumed to be paedomorphic in origin. *Collignonicerites collisniger* n. gen., n. sp. is adult at 18 mm diameter or less and retains the very simple suture of juvenile *Collignoniceras* to maturity (Matsumoto, 1965: text-fig. 6A); it has a phragmocone with umbilical bullae, outer ventrolateral and siphonal clavi, and a smoothing, constricted adult body chamber. *Collignoniceras percarinatum* is also a small species; the largest observed adult is 39 mm in diameter. It most closely

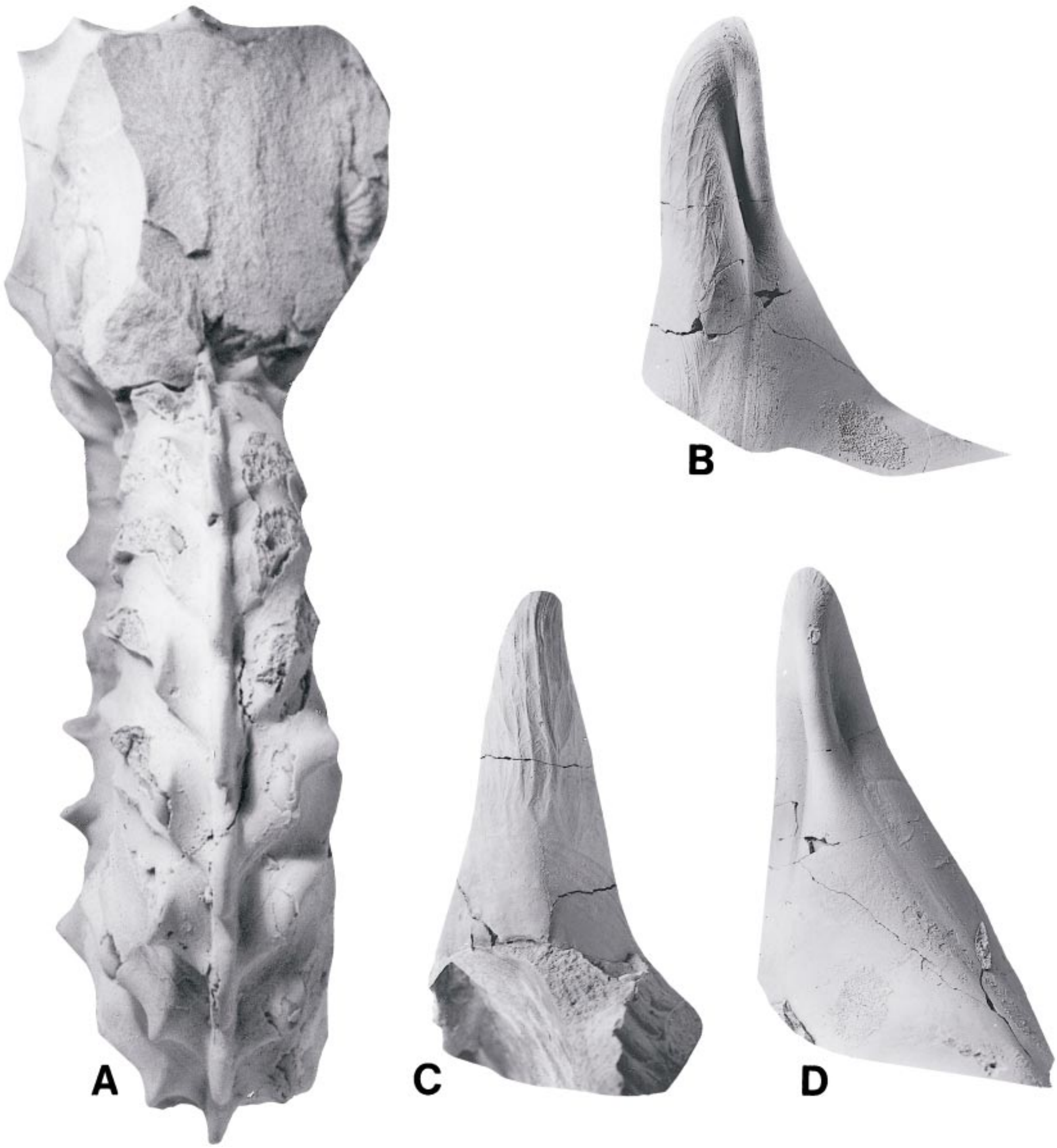

Fig. 20. *Collignoniceras woollgari regulare* (Haas, 1946). **A**. USNM 498238, gracile form from locality 17. **B–D**. isolated ventrolateral spine, BHI 2103, from the lower part of the Carlile Shale in sec. 12, T 9 S, R 1 E, Fall River County, South Dakota. Collected by N. L. Larson. All figures are ×1.

resembles the densicostate, evenly ribbed variants of *woollgari regulare*, but retains the juvenile ornament of these forms to maturity. In western Europe and elsewhere, a series of superficially similar species, referred to the genus *Subprionocyclus* Shimizu, 1932 (see Wright, 1979), occur stratigraphically above *C. woollgari regulare*, as described by Matsumoto (1965: 16).

Whereas *Subprionocyclus* extends into the uppermost Turonian in Europe, Japan, and elsewhere, the later Turonian history of the

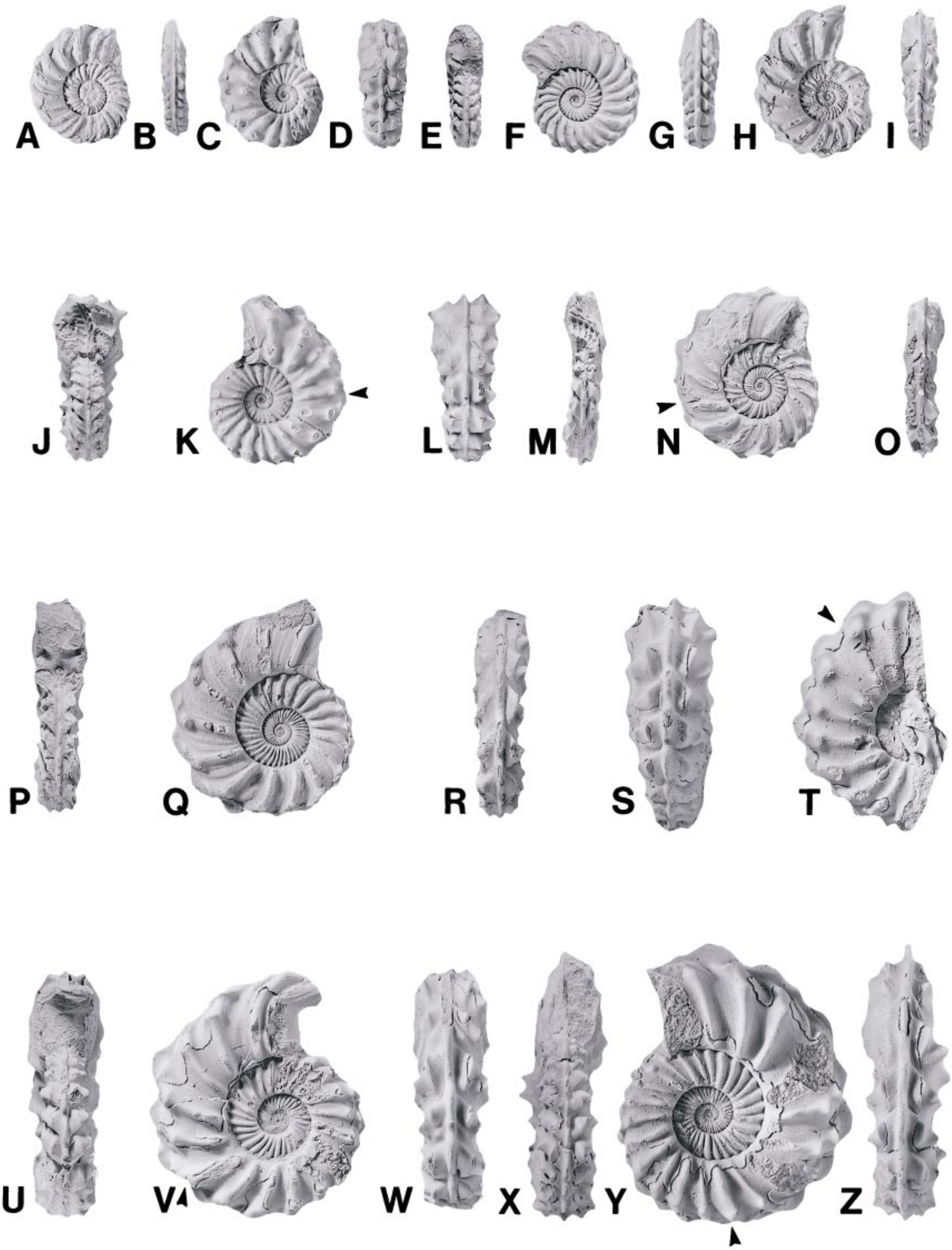

Fig. 21. *Collignoniceras woollgari regulare* (Haas, 1946). **A, B**. USNM 498239, gracile form. **C,**

Collignoniceratinae in the Western Interior is dominated by a succession of species of *Prionocyclus* Meek, 1876, most of which are endemic to the region or are known only as rare individuals in North Africa, western Europe, and Japan. These are medium-sized to large taxa, with adults up to 300 mm in diameter. We have failed to recognize size-linked dimorphism in this genus, due to paucity of complete adults. Ornament is highly variable. The type species of *Collignoniceras* and *Prionocyclus* are very distinct (see below), and juveniles can be distinguished because the keel of *Collignoniceras* has siphonal clavi equal in number to the ventrolateral tubercles, whereas in *Prionocyclus* the serrations outnumber the ribs. *Prionocyclus* also differs from *Collignoniceras* in the persistence to maturity of the marked differentiation of ribbing of the type shown by certain variants of *C. praecox* when young. Finally, *Prionocyclus* is characterized by the appearance of the keel in early ontogeny.

In addition to *Prionocyclus hyatti*, there is a succession of species that differ in details of ornament, as described in the systematic section below: *P. albinus* (Fritsch, 1872), *P. macombi* Meek, 1876, *P. bosquensis* Kennedy, 1988, *P. wyomingensis* Meek, 1876, *P. novimexicanus* (Marcou, 1858), *P. quadratus* Cobban, 1953, *P. germari* (Reuss, 1845), and *P. pluricostatus* n. sp. *Prionocyclites mite* Kennedy, 1988, from the *P. hyatti* Zone of Texas is a diminutive species, reminiscent of *Collignonicerites collisniger* n. gen., n. sp., of the preceding *C. woollgari regulare* Subzone.

Reesidites Wright and Matsumoto, 1954, is rare and only known from a few specimens in the *Prionocyclus wyomingensis* and *Scaphites whitfieldi* zones of New Mexico (Cobban and Kennedy 1988). There are no early Coniacian Collignoniceratinae known from the Western Interior. *Prionocycloceras* Spath, 1926, of the Coniacian is known with certainty from Armenia, North Africa, Madagascar, Venezuela, and Colombia, and possibly from Texas; and *Gauthiericeras* de Grossouvre, 1894, of the upper Coniacian, is known as a rarity in the Western Interior in Montana and New Mexico (Kennedy and Cobban, 1991), as well as occurring in Europe, north, east, and west Africa, Madagascar, New Caledonia, Mexico, Colombia, Peru, Venezuela, and Argentina (Wright, 1996).

VARIATION WITHIN THE COLLIGNONICERATINAE

Haas (1946) observed considerable intraspecific variation within what he referred to as *Prionotropis woollgari* Meek (? *non* Mantell). This form of the species, later referred to as *Collignoniceras woollgari regulare* Haas, 1946, by Cobban and Hook (1979) and Merewether et al. (1979), was subdivided by Haas into the *forma typica*, variety *crassa*, var. *intermedius*, var. *regularis*, var. *tenuicostata*, var. *praecox*, and var. *alata*. These variants were based on details of the ontogeny, ornamentation, and sutures. Haas noted gradation between most of the named forms except his variety *C. woollgari praecox*, which he thought could be a separate species. Most of Haas's material came from a single limestone concretion from the lower part of the Mancos Shale of southern Utah.

During the first of his visits to the United States, Tatsuro Matsumoto was taken by one of us (WAC) on a tour of the Cretaceous rocks of the Black Hills area in eastern Wyoming and western South Dakota. Matsumoto made a large collection of *C. woollgari* (now assigned to *C. woollgari regulare*) from limestone concretions in the lower part of the Carlile Shale at USGS Mesozoic locality 21792 near Newcastle, Wyoming. Matsumoto was impressed by the great variation within the species, and in 1965 Matsumoto assigned his specimens to six groups

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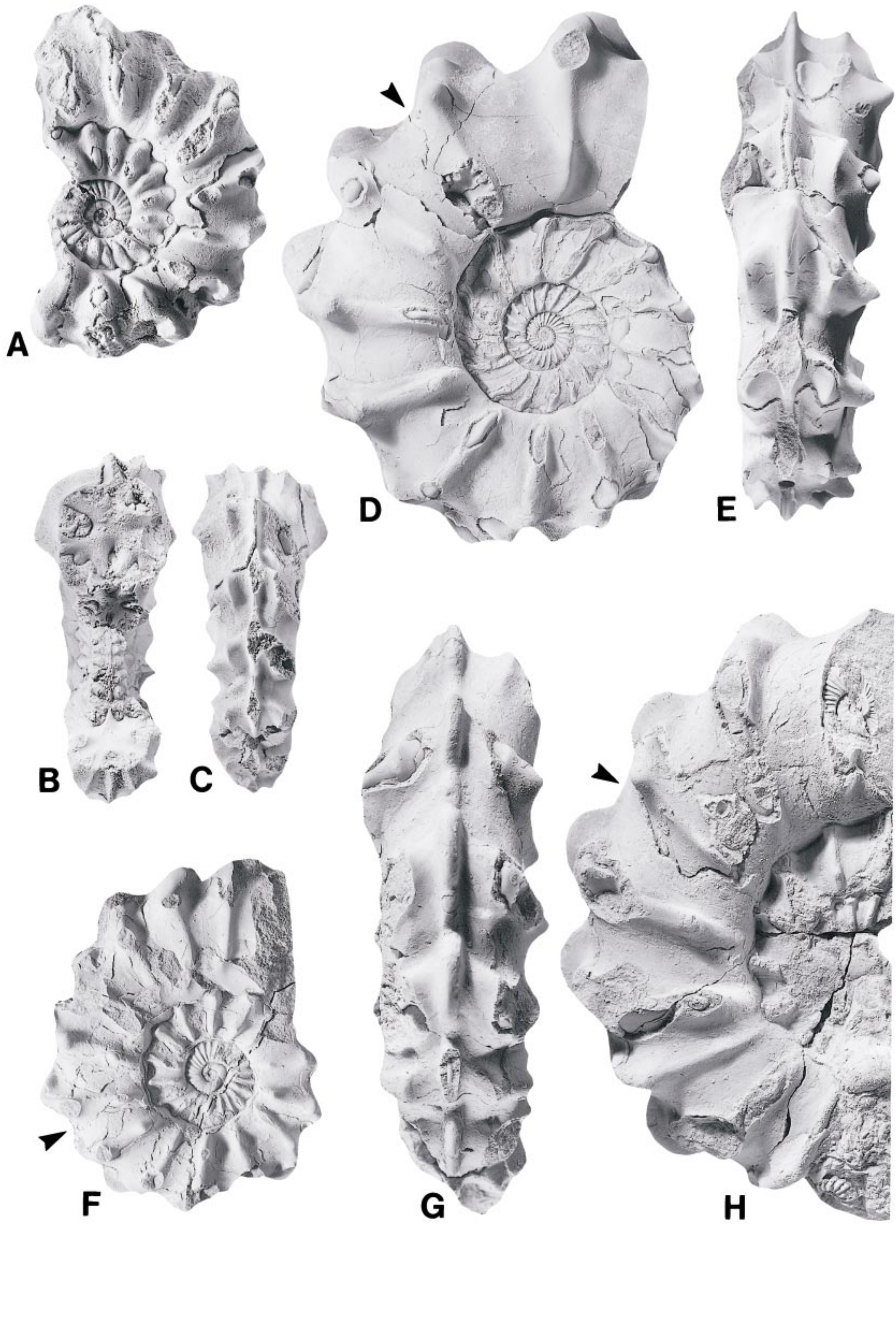
D. USNM 498220, robust form. **E–G**. USNM 498218, gracile form. **H, I**. USNM 498219, gracile form. **J–L**. USNM 498240, robust form. **M–O**. USNM 498241, gracile form. **P–R**. USNM 498222, gracile form. **S, T**. USNM 498242, robust form. **U–W**. USNM 498224, gracile form. **X–Z**. USNM 498243, gracile form. All specimens are from locality 8. All figures are ×1.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lettered A–F, based largely on variation in ornamentation.

Regarding the genus *Prionocyclus*, Haas (1946) noted intraspecific variation within *P. wyomingensis* Meek, 1876. Haas grouped the variations as the *forma typica*, the variety *elegans*, and the variety *robusta*. His variety *elegans* was later determined to be a synonym of *Ammonites novimexicanus* Marcou, 1858, by Hook and Cobban (1979), who demonstrated that Marcou's form was a younger species than *P. wyomingensis.*

The present authors have observed considerable intraspecific variation in all of the larger collections of Collignoniceratinae studied. Most species seem to consist of two major forms, a gracile one that has whorls higher than wide, and a more robust form that has broader whorls, a wider umbilicus, and stronger ornamentation. These may be sexual dimorphs, but we generally lack sufficient complete adult individuals to determine if robust and gracile variants differ in adult size. In the following systematic treatments, these are referred to as gracile and robust forms.

CONVENTIONS

The following abbreviations are used to indicate the repositories of specimens cited in the text:

AMNH American Museum of Natural History, New York
BMNH Natural History Museum, London
OUM Oxford University Museum of Natural History, Oxford
TMM Texas Memorial Museum, Austin
BHI Black Hills Museum of Natural History, Hill City, South Dakota
USNM U.S. National Museum of Natural History, Washington, D.C.

The system of sutural terminology of Wedekind (1916) as propounded by Kullmann and Wiedmann (1970) is used here, with E = external lobe; L = lateral lobe; U = umbilical lobe; and I = internal lobe. All dimensions are given in millimeters, with D = diameter; Wb = whorl breadth; Wh = whorl height; and U = umbilical diameter (fig. 4). In the tables, values in parentheses refer to dimensions as a percentage of diameter. Specimens are photographed in the customary position with the aperture on top although the authors recognize that the animal would have been oriented differently in life. Arrows on photographs indicate the adapical end of the body chamber, if preserved.

SYSTEMATIC PALEONTOLOGY

FAMILY COLLIGNONICERATIDAE WRIGHT AND WRIGHT, 1951

[pro Prionotropidae Zittel, 1895: 430, ex *Prionotropis* Meek, 1876a: 453, *non* Fieber, 1853: 127; = Prionocyclidae Breistroffer, 1947, unpaged, *ex Prionocyclus* Meek, 1871: 298, ineligible as family type]

SUBFAMILY COLLIGNONICERATINAE WRIGHT AND WRIGHT, 1951

Genus *Cibolaites* Cobban and Hook, 1983

TYPE SPECIES: *Cibolaites molenaari* Cobban and Hook, 1983: 16, pl. 2, figs. 1–9; pl. 3, figs. 3–8; pl. 8, figs. 6–8; pl. 13, figs. 1–5; pl. 14; text-figs. 13, 14; lower Turonian *Mammites nodosoides* Zone, west-central New Mexico.

DIAGNOSIS: A medium-size genus, largest known adults 120 mm in diameter; dimorphism not demonstrated. Coiling involute with small umbilicus, whorl section compressed to depressed, intercostal section with convergent sides and fastigiate venter, costal section markedly concave between tubercles. Strong conical umbilical bullae give rise to primary ribs singly or in pairs with shorter, intercalated ribs, all with ventrolateral and siphonal clavi on phragmocone. Umbilical bullae decline on the adult body chamber, which is flat-sided with crowded weak primary and intercalated

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Fig. 22. *Collignoniceras woollgari regulare* (Haas, 1946). **A–C**. USNM 498244, robust form from locality 8. **D, E**. USNM 498245; **F**. USNM 498246; **G, H.** USNM 498247, all robust forms from locality 7. All figures are ×1.

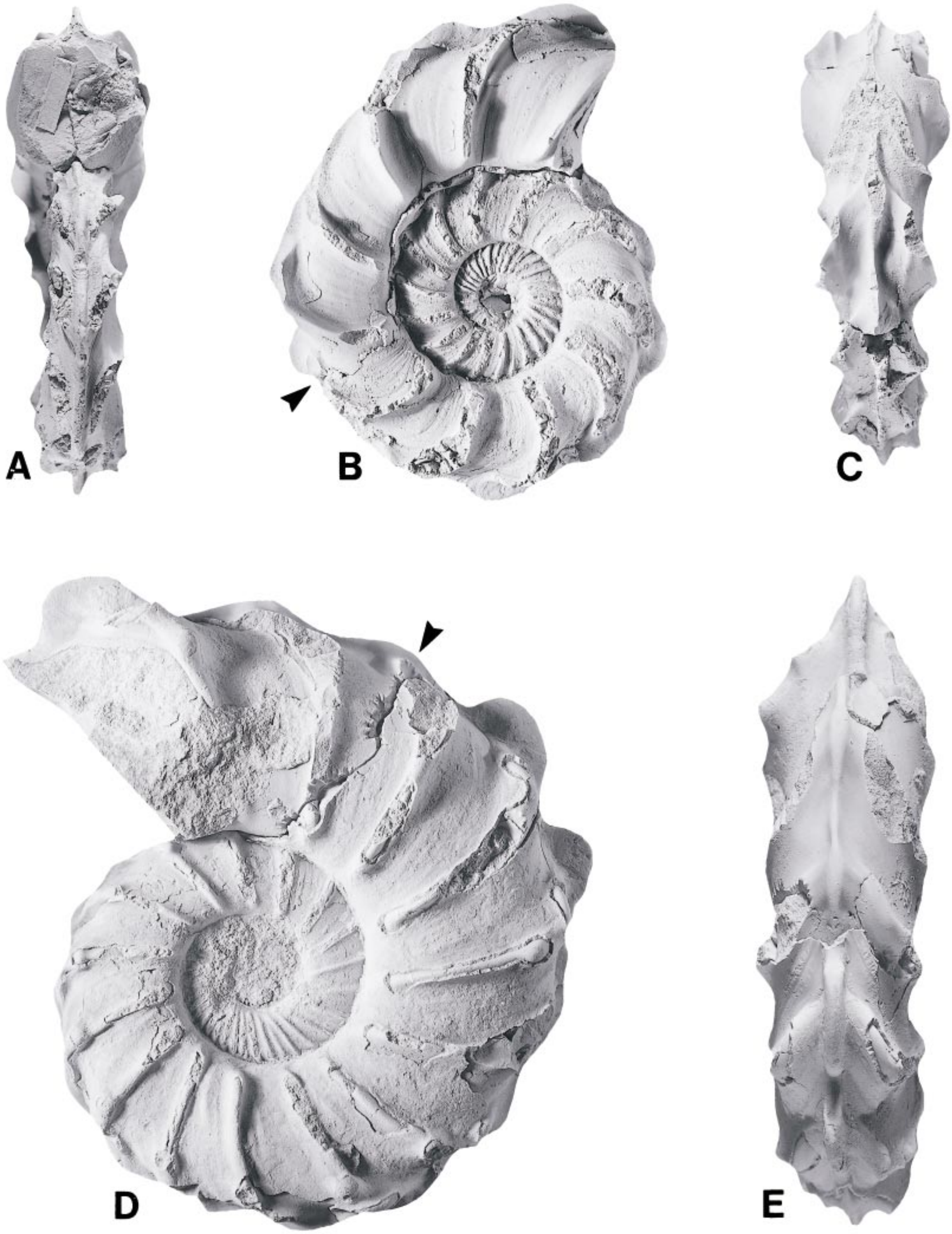

Fig. 23. *Collignoniceras woollgari regulare* (Haas, 1946). **A–C**. USNM 498226, gracile form from locality 8. **D, E**. USNM 252723, gracile form from locality 7. All figures are ×1.

Fig. 24. *Collignoniceras woollgari regulare* (Haas, 1946). USNM 420012, robust form from locality 62. Figures are ×0.80.

ribs; ventrolateral and siphonal tubercles decline progressively and the venter flattens towards the adult aperture.

Suture relatively simple with broad, little-divided saddles and narrower, rectangular lobes.

DISCUSSION: Coarse tuberculation and presence of only a single row of ventrolateral tubercles distinguishes *Cibolaites* from all other genera currently referred to the Collignoniceratinae. *Cibolaites* superficially resembles *Barroisiceras* de Grossouvre, 1894, and *Subbarroisiceras* Basse, 1946, of the upper Turonian–Coniacian Barroisiceratinae. However, they differ in sutural characteristics, while both are more involute than *Cibolaites*, with smaller umbilici and crenulate keels; in *Cibolaites* there is no continuous keel and the siphonal clavi are separated by smooth interspaces.

Fig. 25. *Collignoniceras woollgari regulare* (Haas, 1946). USNM 498248, robust form from locality 14. Figures are ×0.80.

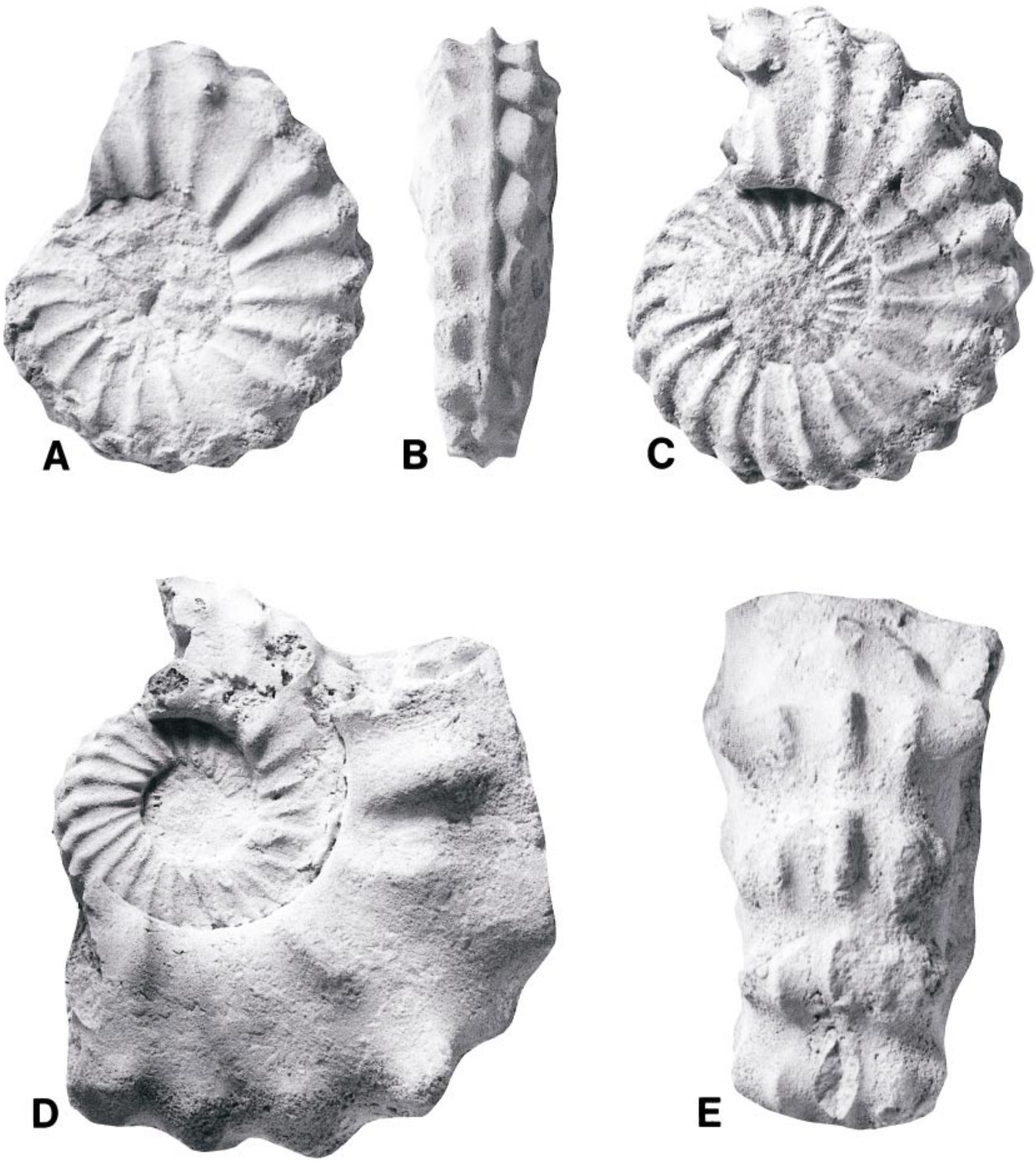

Fig. 26. *Collignoniceras woollgari regulare* (Haas, 1946). **A, B**. Muséum National d'Histoire Naturelle, Paris, no. 6778 (*ex* d'Orbigny Collection), from the Middle Turonian of Poncé, Sarthe, France. **C**. Faculté des Sciences, Rennes, no. C273, also from Poncé. **D, E**. Same collection as A, B, no. W1, from ''Le Mans, Sarthe,'' France. All figures are ×1.

OCCURRENCE: Upper Cenomanian *Neocardioceras juddii* Zone in Devon, England and Aube, France; lower Turonian *Mammites nodosoides* Zone, immediately below first appearance of *C. woollgari woollgari* of the middle Turonian in west-central New Mexico; *M. nodosoides* Zone, N.W. Germany; also recorded from northern Spain (Kaplan, 1988) and from Tunisia (Chancellor et al., 1994).

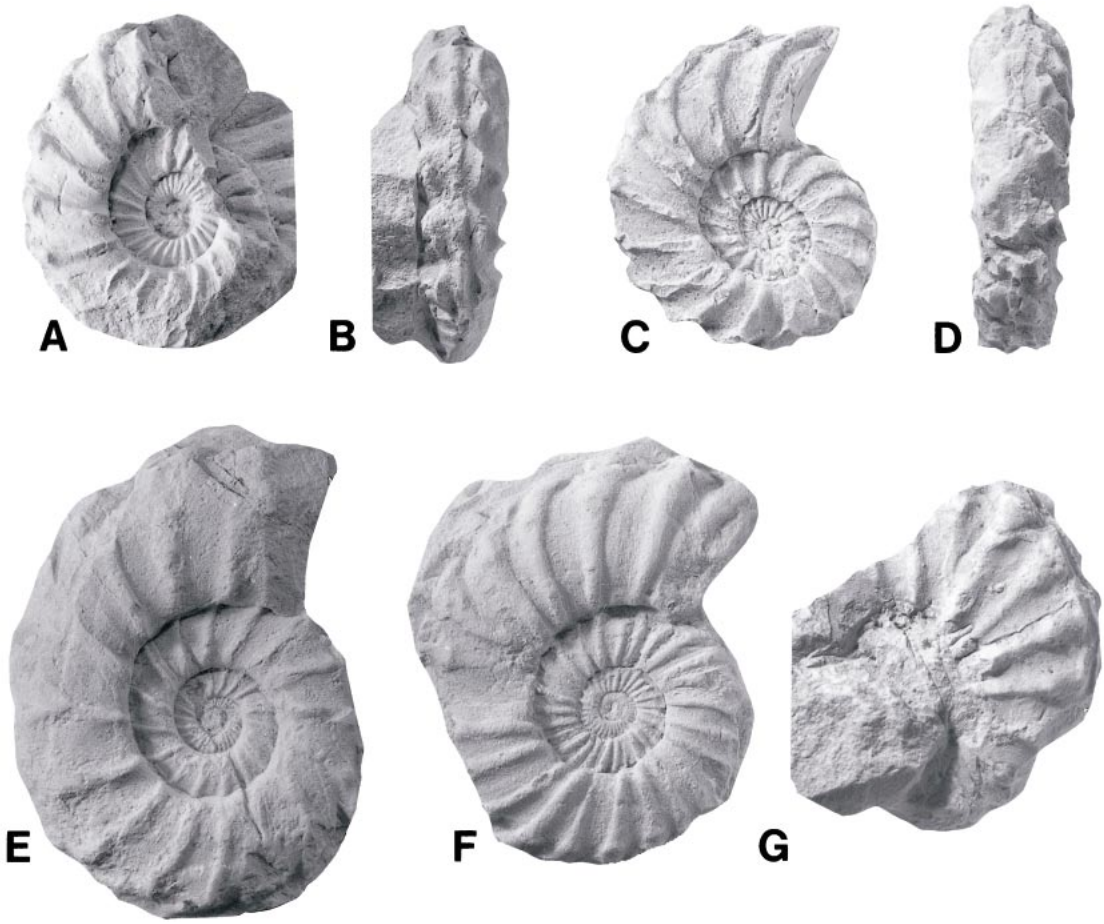

Fig. 27. *Collignoniceras woollgari regulare* (Haas, 1946). **A, B**. BMNH 4863, from ''near Lewes,'' Sussex, England (*ex* J. de C. Sowerby Collection). **C, D**. BMNH 4863a, from the same locality. **E**. paralectotype BMNH 5742b. **F**. Paralectotype BMNH 5742a, both from near Lewes, Sussex. **G**. BMNH C82268, from the Middle Turonian Middle Chalk, upper *Terebratulina lata* Zone, Mickleham Bypass, Surrey, England. All figures are ×1.

Cibolaites molenaari Cobban and Hook, 1983

Figures 5–8

Collignoniceras sp. Wright and Kennedy, 1981: 107, pl. 8, fig. 17.

Cibolaites molenaari Cobban and Hook, 1983: 16, pl. 2, figs. 1–9; pl. 3, figs. 3–8; pl. 8, figs. 6–8; pl. 13, figs. 1–5; pl. 14; text-figs. 13, 14.

Cibolaites molenaari Cobban and Hook. Kennedy et al., 1986: 209, text-fig. 5i, j, k, l.

Cibolaites sp. Kaplan, 1988: 23, pl. 6, figs. 4, 5.

Cibolaites molenaari Cobban and Hook. Cobban and Hook, 1989: figs. 8c, d.

Cibolaites molenaari Cobban and Hook, 1983. Reyment and Kennedy, 2001: fig. 1a, b.

TYPES: Holotype is USNM 328766 (fig. 5), from the Rio Salado Tongue of the Mancos Shale, lower Turonian *Mammites nodosoides* Zone, immediately below the first occurrence of *Collignoniceras woollgari woollgari* of

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Fig. 28. *Collignoniceras woollgari regulare* (Haas, 1946). Muséum National d'Histoire Naturelle, Paris, no. W2. 1904–32, from ''Le Mans, Sarthe,'' France. Figures are ×1.

Fig. 29. *Collignoniceras woollgari regulare* (Haas, 1946). Muséum National d'Histoire Naturelle, Paris, 102–27, from the Middle Turonian of Poncé, Sarthe, France. Reduced ×0.625.

the middle Turonian at USGS Mesozoic locality D11208, NE1/4 sec. 36, T. 6 N, R. 19 W, Cibola County, New Mexico. Paratypes USNM 328752–328767, 329013, are from the Rio Salado Tongue at this and nearby localities.

DIAGNOSIS: Characteristic features of this moderate-size species are the strong, nodate umbilical tubercles during early and middle growth and the equal numbers of prominent siphonal clavi and clavate inner ventrolateral tubercles.

DESCRIPTION: The early whorls are smooth to a diameter of 5 mm, with rounded flanks

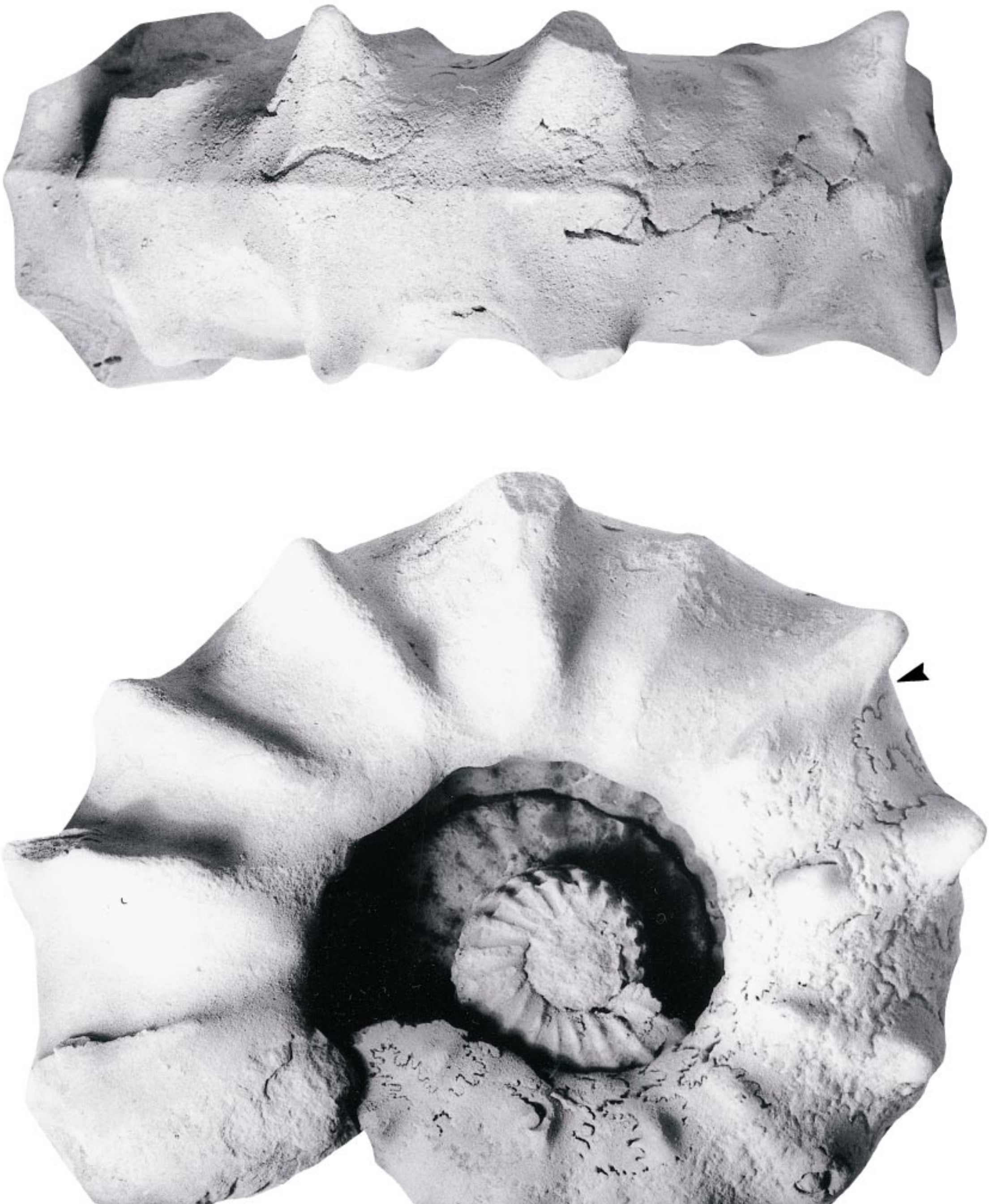

Fig. 30. *Collignoniceras woollgari regulare* (Haas, 1946). Muséum National d'Histoire Naturelle, Paris, W. 22, 6778 (*ex* d'Orbigny Collection), from the Middle Turonian of Poncé, Sarthe, France. Reduced ×0.625.

Fig. 31. *Collignoniceras woollgari regulare* (Haas, 1946). Muséum National d'Histoire Naturelle, Paris, 1946–19, from the Middle Turonian of Sainte-Maure-de-Touraine, Indre et Loire, France. Reduced approximately ×0.7.

and venter. Low umbilical bullae, 14 per whorl, appear between 5 and 7 mm diameter; ventrolateral and siphonal tubercles appear around 10 mm diameter. As size increases (figs. 6, 7), the number of bullae decreases to as few as seven per whorl in middle growth. Coiling is fairly involute, with a deep umbilicus. Two broad prorsiradiate to

Fig. 32. *Collignoniceras woollgari regulare* (Haas, 1946). Muséum National d'Histoire Naturelle, Paris, 1946–19, from the Middle Turonian of Sainte-Maure-de-Touraine, Indre et Loire, France. Reduced approximately ×0.7.

rectiradiate ribs generally arise from each bulla, which vary in strength within and between specimens. The ribs are broad, rounded, and terminate in strong ventrolateral clavi; occasional intercalated ribs arise around midflank or below and bear clavi of comparable strength to give a total of 22 or so ribs per whorl at diameters of up to 65 mm. Each

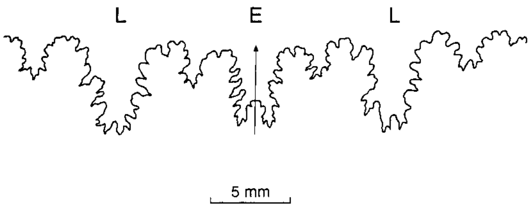

Fig. 33. External suture of *Collignoniceras woollgari regulare* (Haas, 1946). Copy of Haas, 1946: figure 83.

ventrolateral clavus gives rise to a broad, low prorsiradiate rib that arches forward across the venter to form an obtuse chevron with a strong siphonal clavus at the apex. In profile, the adapical slope of this clavus is low, the adapertural slope much steeper, giving the clavus a distinctly asymmetric profile. At this stage the costal and intercostal whorl sections vary from compressed to depressed (see table 1); the greatest breadth in intercostal section is just outside the umbilical shoulder. The inner flanks are broadly rounded, the outer flanks flattened and convergent, and the venter fastigiate. The costal section has the greatest breadth at the umbilical bullae and the flanks are concave between tubercles; the venter is markedly fastigiate. On the later parts of the phragmocone as well as on the adult body chamber, the ornament is progressively modified (fig. 5); first, the umbilical bullae decline and ultimately disappear. The ventrolateral and siphonal clavi weaken markedly, but are still present, though very weak, immediately adapical of the adult aperture. As they decline, the venter broadens and rounds. On the body chamber, the flanks flatten and the whorl section becomes rectangular, with low, weak, prorsiradiate ribs, irregularly long and short, the latter of variable length. Part or all of the body chamber is preserved on 46 specimens. Diameter at the last septum ranges from 44 to 94 mm, without any clear clustering into size classes or indication of size dimorphism. Suture with broad, bifid E/L, narrow, bifid L, slightly broader L/U_2, and much narrower U_2 (fig. 8).

Cibolaites molenaari occurs as gracile and robust forms, as indicated in the figure captions, although the distinctions between them are not as pronounced as in species of *Collignoniceras* and *Prionocyclus*. The holotype and paratypes figured by Cobban and Hook (1983) can be assigned to the following forms: gracile form, pl. 2, figs. 1–6, pl. 3, figs. 3, 4, 6–8, pl. 14, figs. 1–15; robust form, pl. 2, figs. 7–9, pl. 3, fig. 5, pl. 8, figs. 6–8, pl. 13, figs. 1–5.

DISCUSSION: Coarse ornament and presence of only a single row of ventrolateral tubercles at all stages distinguishes *C. molenaari* from all of the collignoniceratids described here. Body chamber characters sep-

TABLE 2
Dimensions of *Collignoniceras woollgari regulare* (Haas, 1946)[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
USNM 489217	Costal	19.3 (100)	4.4 (22.8)	8.6 (44.6)	0.51	5.6 (29.0)
USNM 489218	Costal	21.8 (100)	6.6 (30.3)	8.3 (38.0)	0.80	7.9 (36.2)
USNM 498219	Costal	23.4 (100)	6.3 (26.9)	9.6 (41.0)	0.66	8.0 (34.1)
USNM 498220	Costal	22.1 (100)	8.2 (37.1)	8.6 (38.9)	0.95	7.5 (33.9)
USNM 498221	Costal	23.3 (100)	8.5 (36.5)	9.8 (42.1)	0.87	7.2 (30.9)
USNM 498222	Costal	32.2 (100)	8.6 (26.7)	11.8 (36.6)	0.73	11.3 (35.1)
	Intercostal	29.9 (100)	6.0 (20.0)	10.5 (23.7)	0.57	11.3 (37.8)
USNM 498223	Costal	37.7 (100)	13.7 (36.3)	15.2 (40.3)	0.90	11.4 (30.2)
	Intercostal	34.6 (100)	9.8 (28.3)	11.9 (34.4)	0.82	11.4 (32.9)
USNM 498224	Costal	39.0 (100)	12.6 (32.3)	12.4 (31.8)	1.02	14.6 (37.4)
	Intercostal	37.5 (100)	7.7 (20.5)	10.1 (26.9)	0.76	14.6 (38.9)
USNM 498225	Costal	75.3 (100)	29.5 (39.2)	28.0 (37.2)	1.05	25.9 (34.4)
	Intercostal	67.8 (100)	25.0 (36.9)	26.2 (38.6)	0.95	25.9 (38.2)
USNM 498226	Costal	76.2 (100)	23.0 (30.2)	25.4 (33.3)	0.91	32.6 (42.8)
	Intercostal	72.2 (100)	15.9 (22.0)	21.5 (29.8)	0.74	32.6 (45.2)

[a] See table 1 for explanation of symbols.

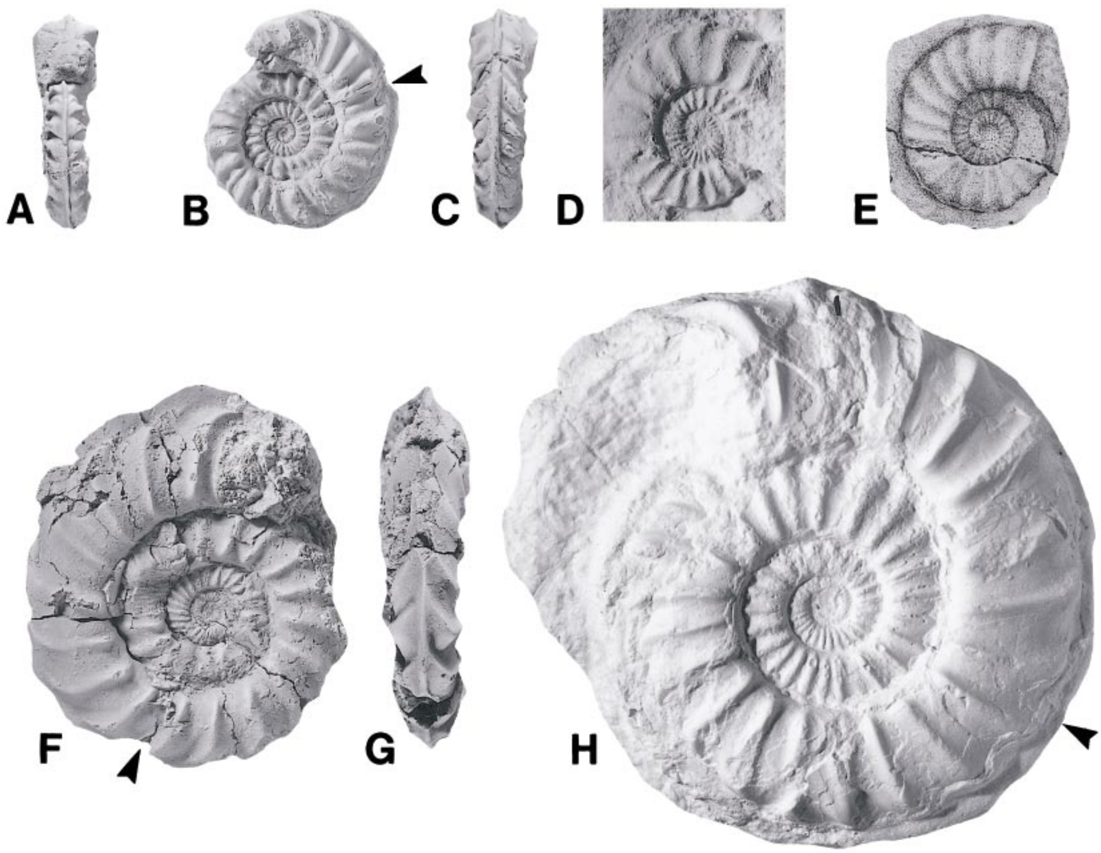

Fig. 34. **A–C**. *Collignoniceras jorgenseni* n. sp., USNM 498250, a paratype, robust form from locality 20. **D–H**. *Collignoniceras vermilionense* (Meek and Hayden, 1860). **D**. cast of holotype, USNM 224; **E**. Copy of original figure of Meek, 1876a: plate 7, figure 2. Original is from a limestone concretion in the Carlile Shale, probably the middle Turonian *Collignoniceras praecox* Zone, on the Missouri River opposite the mouth of Vermillion (formerly Vermilion) River in Dixon County, Nebraska. **F, G**. USNM 299166, gracile form from locality 21. **H**. S. Jorgensen Collection CO1970a, Carlile Shale, *Collignoniceras praecox* Zone, dredged from Missouri River during natural gas pipeline construction at Yankton, South Dakota. All figures are ×1.

arate it from *Lecointriceras fleuriausianum* (D'Orbigny, 1841) (fig. 9) as discussed above.

OCCURRENCE: Upper Cenomanian *Neocardioceras juddii* Zone in Devon, England, and Aube, France; lower Turonian *Mammites nodosoides* Zone in west-central New Mexico and northeastern Arizona; N.W. Germany.

Genus *Collignoniceras* Breistroffer, 1947

[ICZN, 1968, Opinion 861, name no. 1798; *pro Prionotropis* Meek, 1876a: 453, *non* Fieber, 1853: 127; = *Selwynoceras* Warren and Stelck, 1940: 151; *non Collignoniceras* Van Hoepen, 1955: 361].

TYPE SPECIES: *Ammonites woollgari* Mantell, 1822: 197, pl. 21, fig. 16; pl. 22, fig. 7, by the original designation of Meek, 1876a: 453, as type species of *Prionotropis* Meek, 1876a (*non* Fieber, 1853) for which Breistroffer (1947, unpaged) proposed *Collignoniceras* as *nomen novum*, from the Turonian of England.

DIAGNOSIS: ''Medium-sized, moderately involute to evolute ammonites. Early whorls compressed, parallel-sided, ornamented by crowded or sparse, prorsiradiate, straight or

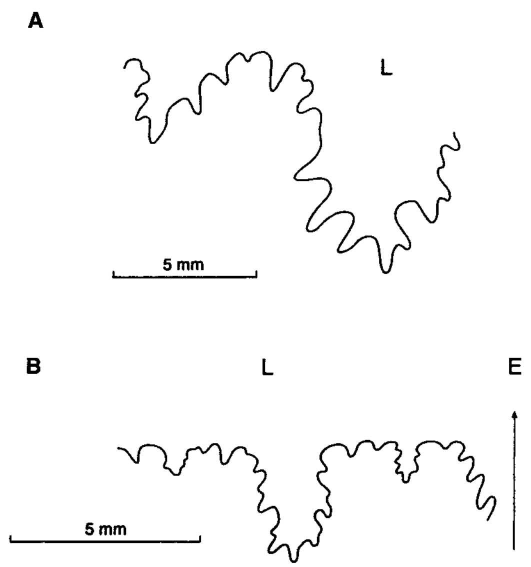

Fig. 35. **A**. Partial external suture of *Collignoniceras vermilionense* (Meek and Hayden, 1860). S. Jorgensen Collection no. CO1970A from the Middle Turonian *C. praecox* Zone, concretion dredged from Missouri River during natural gas pipeline construction at Yankton, South Dakota. **B**. *Collignoniceras jorgenseni*, n. sp. Partial external suture of paratype USNM 498253, collected by S. D. Jorgensen from the Middle Turonian *C. praecox* Zone, Carlile Shale at locality 16.

flexuous ribs, mostly long, with weak to strong umbilical bullae. All ribs bear in the early stages outer ventrolateral tubercles in addition to siphonal clavi. This style of ornament is, in some species, retained to maturity. In most, however, the ribs coarsen, become widely spaced, with strong to weak umbilical tubercles (which migrate progressively outward from the umbilical margin), prominent inner and outer ventrolateral tubercles, which may fuse into a massive horn or flared rib, from which commonly arise pairs of low ribs joining siphonal clavi more numerous than the ventrolateral and linked into a more or less continuous keel. Rarely the ornament is greatly reduced on the body whorl. Sutures little incised, with massive saddles" (Wright and Kennedy, 1981: 102).

DISCUSSION: See Kennedy et al. (1980: 558) and Wright and Kennedy (1981: 102).

OCCURRENCE: Middle to lower upper Turonian, England, France, Germany, Czech Republic, Poland, Roumania, eastwards to Turkmenistan, Japan, California, northern Mexico, the U.S. and Canadian Interiors, Greenland, North Africa, Colombia, south India, northern Australia.

Collignoniceras woollgari woollgari (Mantell, 1822)

Figures 10–15

Ammonites woollgari Mantell, 1822: 197, pl. 21, fig. 16; pl. 22, fig. 7.

Collignoniceras woolgari (sic) (Mantell) (early form). Merewether et al., 1979: pl. 3, figs. 9, 10.

Collignoniceras woollgari woollgari (Mantell). Cobban and Hook, 1979: 21, pl. 1, figs. 1–11; pl. 2, figs. 5–22; pl. 4, figs. 11, 12; pl. 5, figs. 13–16; pl. 12, figs. 1, 2 (with synonymy).

Collignoniceras woollgari (Mantell). Kennedy et al., 1980: 560 (*pars*), pl. 62; pl. 63, figs. 1–4, 7–12, *non* 5, 6; pl. 64; pl. 65, figs. 1–3; text-fig. 2, ?3, 4c, d, *non* 4a, b.

Collignoniceras woollgari (Mantell, 1822). Wright and Kennedy, 1981: 103, pl. 28, fig. 3, *non* 1, 2; pl. 29, fig. 5, *non* 1–4, 6, 7; pl. 30, fig. 1, *non* 2, 3.

Collignoniceras woollgari (Mantell, 1822). Amédro and Badillet, 1982: 131, pl. 5, fig. 1.

Collignoniceras woollgari (Mantell). Amédro et al., 1982: 30, pl. 1, figs. 5–7.

Collignoniceras woollgari (Mantell). Amédro and Hancock, 1985: fig. 9e, f.

TABLE 3

Dimensions of *Collignoniceras vermilionense* (Meek and Hayden, 1860)[a]

Specimen	D	Wb	Wh	Wb:Wh	U
Holotype (from cast), USNM 224	26.3 (100)	— (—)	8.3 (31.6)	—	12.2 (46.4)
USNM 299166	56.0 (100)	— (—)	17.4 (31.1)	—	25.5 (45.5)
Jorgen. Co1970A	83.8 (100)	— (—)	26.4 (31.5)	—	37.7 (45.0)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.

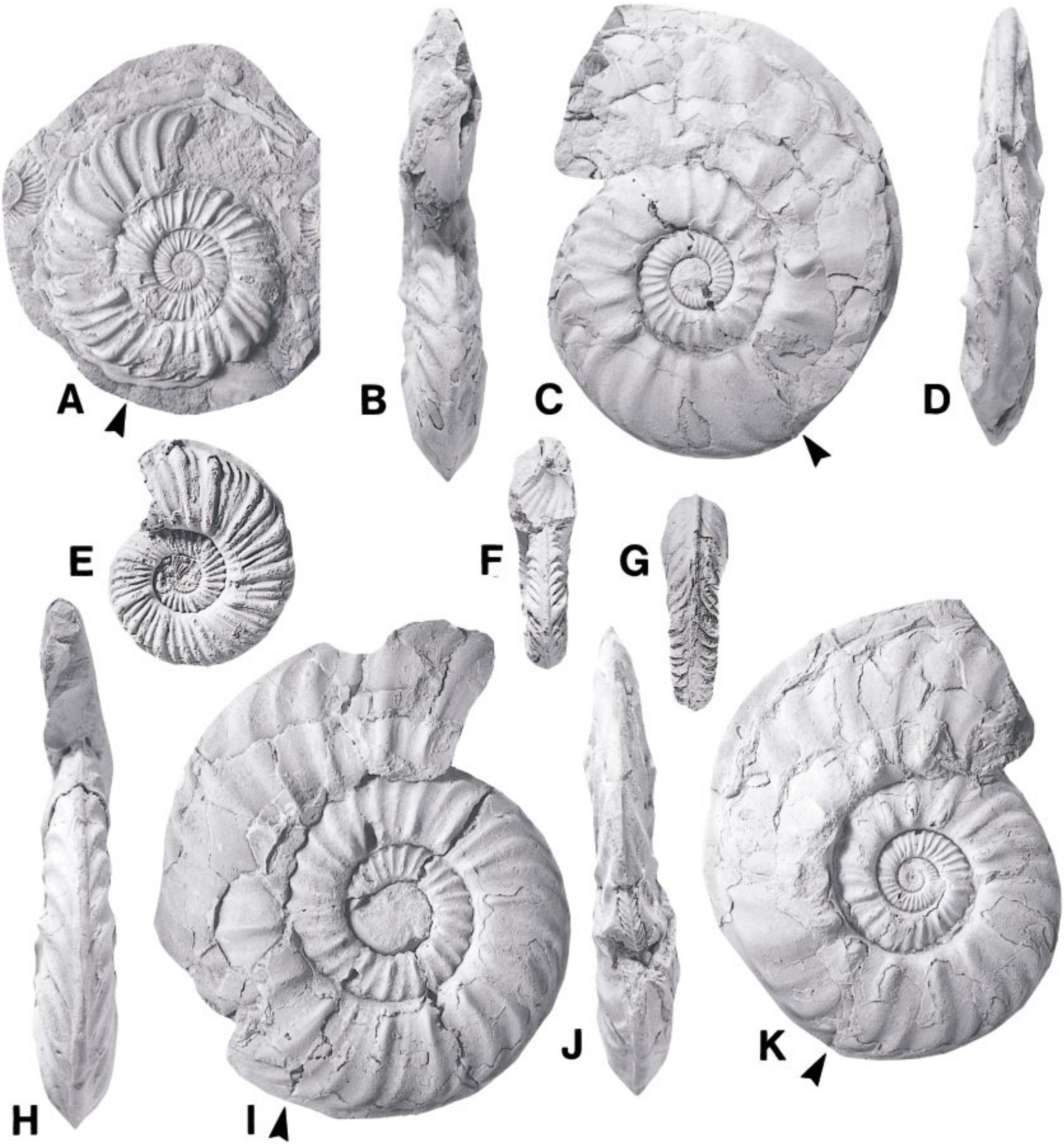

Fig. 36. *Collignoniceras jorgenseni*, n. sp. **A**. holotype, USNM 498249, robust form; **B–D, K**. Paratype USNM 498253, gracile form; both from locality 16. **E–G**. USNM 356918, robust form from the lower part of the Carlile Shale, center of sec. 35, T 8S, R 1E, Fall River County, South Dakota. **H–J**. Paratype USNM 498254, gracile form from locality 16. All figures are ×1.

Collignoniceras woollgari woollgari (Mantell). Cobban, 1986: 81, figs. 6j, k; 7k, l.

Collignoniceras woollgari woollgari (Mantell, 1822). Kennedy and Cobban, 1988: 604, figs. 7.14, 15.

Collignoniceras woollgari (Mantell, 1822). Kaplan, 1988: 11, pl. 1, fig. 1; pl. 2, figs. 1–7; pl. 7, fig. 1.

Collignoniceras woollgari woollgari (Mantell, 1822). Kennedy et al., 1989: 86, fig. 24a–c, h–l.

Collignoniceras woollgari (Mantell, 1822). Cobban and Hook, 1989: fig. 9q, r.


A
A
B
B

Collignoniceras woollgari (Mantell, 1822). Amédro, 1990: 269, pl. 24, fig. 2.
Collignoniceras woollgari woollgari (Mantell, 1822). Emerson et al., 1994: 208, unnumbered figure.
Collignoniceras woollgari woollgari (Mantell, 1822). Reyment and Kennedy, 2001: fig. 1c, d.

TYPES: Lectotype (fig. 10) is BMNH 5682, the original of Mantell, 1822: pl. 21, fig. 16, from the Middle Chalk of Lewes, Sussex, England; designated by Wright and Wright, 1951: 35. Presumed paralectotypes (fig. 27E, F) are BMNH C5742a, b, from the same locality.

DIAGNOSIS: This moderately evolute subspecies has prorsiradiate to rectiradiate primary and secondary ribs that support bullate inner ventrolateral tubercles and clavate outer ventrolateral tubercles matched by siphonal clavi.

DISCUSSION: Cobban and Hook (1979) provided an account of *C. woollgari woollgari* from New Mexico, and Kennedy et al. (1980) and Wright and Kennedy (1981) reviewed the European material at length. We illustrate here a selection of European, Mexican, and U.S. Western Interior material (figs. 10–15) for comparison with *C. woollgari regulare*, described below, where features distinguishing it from the nominate subspecies are outlined. Gracile and robust forms of *C. woollgari woollgari* are present, as indicated in the figure captions. Specimens figured by Cobban and Hook (1979) include gracile forms (pl. 1, figs. 1–3, 10, 11; pl. 2, figs. 5–19; pl. 5, figs. 13–16), and robust forms (pl. 1, figs. 4–9; pl. 2, figs. 20–22; pl. 4, figs. 11, 12; pl. 12, figs. 1, 2).

OCCURRENCE: *Collignoniceras woollgari woollgari* Subzone, widespread in the U.S. Western Interior from Wyoming to the Rio Grande; California, northern Mexico, Europe, east to Turkmenistan; Tunisia, Japan, and northern Australia.

Collignoniceras woollgari regulare (Haas, 1946)

Figures 17–33, 49L

Prionocyclus (*Prionotropis*) *woolgari* (sic) (Mantell). Meek, 1876a: 455, pl. 6, fig. 2; pl. 7, figs. 1, 3.
Prionocyclus (*Prionotropis*) *woolgari* (sic) (Mantell). Boyle, 1893: 243.
Prionotropis woolgari (sic) Mantell. Stanton, 1894: 174, pl. 42, figs. 1–4.
Prionotropis woolgari (sic) Mantell. Logan, 1898: 466, pl. 102, figs. 1–4.
Prionotropis woolgari (sic) Mantell. Roman, 1938: 455, pl. 46, fig. 434b, c.
Prionotropis graysonensis (Shumard). Moreman, 1942: 213 (*pars*).
Prionotropis woolgari (sic) (Mantell). Shimer and Shrock, 1944: 593, pl. 247, figs. 1, 2.
Prionotropis woollgari (Mantell) and varieties. Haas, 1946: 150, pls. 11, 12; pl. 13, figs. 1–3, 5–18 (*non* 4, 19); pl. 14, figs. 1–10, 12–16 (*non* 11); pl. 15, figs. 1–10; pl. 16, figs. 1–21 (*non* 22–33); *non* pl. 17; pl. 18, figs. 1, 3–7 (*non* 8, 9); text-figs. 1–4, 6–14, 19–79, 80–83, 91.
Prionotropis Adkins and Lozo, 1951: pl. 5, figs. 4–9.
Collignoniceras woollgari (Mantell). Cobban et al., 1956: 1270, fig. 1b–h.
Collignoniceras woollgari (Mantell). Matsumoto and Miller, 1958: 353, pl. 44, figs. 1–6; pl. 45, fig. 1.
Collignoniceras woollgari (Mantell). Matsumoto, 1959: 105, figs. 55–57.
Collignoniceras woollgari (Mantell). Hattin, 1962: pl. 12, figs. D, E.
Collignoniceras woollgari (Mantell). Hattin, 1965: fig. 4–3.
Collignoniceras woollgari (Mantell). Matsumoto, 1965: 11, pl. 1, figs. 1–6; pl. 2, figs. 1–3; pl. 3, figs. 1, 2; text-fig. 6.
Prionocyclus (*Collignoniceras*) *woolgari* (sic) (Mantell). Jeletzky, 1970: pl. 26, fig. 9a, b.
Prionocyclus (*Prionocyclus*) *wyomingensis* Meek var. *robusta* Haas. Jeletzky, 1970: pl. 26, fig. 3.
Prionocyclus (*Prionocyclus*) *wyomingensis* Meek var. *elegans* Haas. Jeletzky, 1970: pl. 6, fig. 8a, b.
Collignoniceras woollgari (Mantell). Cobban and Scott, 1972: 94, pl. 14, fig. 5; pl. 30, fig. 1; pl. 37, figs. 9, 10.

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Fig. 37. *Collignoniceras jorgenseni*, n. sp. **(A)** and *Collignoniceras vermilionense* (Meek and Hayden, 1860) **(B)**. USNM 498255, from locality 16. Figure is ×0.95.

TABLE 4
Dimensions of *Collignoniceras jorgenseni* n. sp.[a]

Specimen	D	Wb	Wh	Wb:Wh	U
USNM 498249	38.3 (100)	— (—)	13.5 (38.3)	—	16.2 (42.2)
USNM 498250	30.7 (100)	9.0 (29.3)	10.5 (34.2)	0.86	15.2 (49.5)
USNM 498251	33.7 (100)	11.2 (33.2)	13.0 (38.6)	0.86	13.9 (41.2)
USNM 498252	40.5 (100)	10.7 (26.4)	15.0 (37.0)	0.71	16.9 (41.7)
USNM 498253	44.0 (100)	— (—)	17.0 (38.6)	—	16.8 (38.2)
USNM 498254	51.0 (100)	— (—)	17.7 (34.7)	—	21.2 (41.6)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.

Collignoniceras woollgari (Mantell). Hattin, 1975a: pl. 10, figs. N, P–R.
Collignoniceras woollgari (Mantell). Hattin, 1975b: pl. 2, figs. 1–3.
Collignoniceras woollgari (Mantell). Cobban, 1976: 120, pl. 1, fig. 7.
Collignoniceras woollgari (Mantell). Kennedy and Cobban, 1976: 46, pl. 10, figs. 1, 2.
Collignoniceras woollgari (Mantell). Kauffman, 1977: pl. 22, figs. 4–6, pl. 26, fig. 6.
Collignoniceras woollgari (Mantell). Hattin, 1977: 189, fig. 8.5.
Collignoniceras woollgari Mantell. Kauffman et al., 1978: pl. 5, figs. 4–6.
Collignoniceras woollgari (Mantell). Hattin and Siemers, 1978: figs. 7.10, 10.5.
Collignoniceras woollgari (Mantell) (late form). Merewether et al., 1979: pl. 3, figs. 4, 5.
Collignoniceras woollgari regulare (Haas). Cobban and Hook, 1979: 22, pl. 3, figs. 1–14; pl. 12, fig. 3.
Collignoniceras woollgari (Mantell). Kennedy et al., 1980: 560 (*pars*), pl. 63, figs. 5, 6; pl. 65, figs. 4–8.
Collignoniceras woollgari (Mantell, 1822). Wright and Kennedy, 1981: 103 (*pars*), pl. 28, fig. 2; pl. 29, figs. 2, 6, 7; pl. 30, fig. 3.
Collignoniceras woollgari regulare (Haas). Cobban, 1983: 16, pl. 15, figs. 2–4, 7–11.
Collignoniceras woollgari regulare (Haas). Cobban, 1984b: 14, pl. 2, figs. 6, 7.
Collignoniceras woollgari (Mantell). Kennedy, 1986: pl. 13, figs. 1–3.
Collignoniceras woollgari (Mantell). Wright and Kennedy, 1987: 166, pl. 34, figs. 5, 6.
Collignoniceras woollgari regulare (Haas). Kennedy, 1988: 74, pl. 14, figs. 1, 2, 4, 5, 10, 11.
Collignoniceras woollgari regulare (Haas). Kennedy and Cobban, 1988: 606, figs. 7.9–7.15.
Collignoniceras woollgari (Mantell, 1822) *regulare* (Haas, 1946). Kennedy et al., 1989: 88, figs. 21, 22, 23, 24d.
Collignoniceras woollgari (Mantell). Kennedy, 1989: 257, fig. 7.
Collignoniceras woollgari (Mantell). Cobban, 1990: B9, pl. 5, figs. 6–13.
Collignoniceras woollgari regulare (Haas, 1946). Emerson et al., 1994: 209, 378.
Collignoniceras woollgari regulare (Haas, 1946). Reyment and Kennedy, 2001: fig. 1e–j.

TYPES: Holotype, by original designation, South Dakota State School of Mines Collection no. 1470, the original of Haas, 1946, plate 16, figures 14, 16; text-figs. 80, 81, from an unknown horizon and locality in the Black Hills area (fide Haas, 1946: 198).

MATERIAL: The present description is based on more than 500 specimens from USGS Mesozoic locality 21792, limestone concretions 18.9–21.3 m above the base of the Carlile Shale, middle Turonian *Collignoniceras woollgari* Zone, *regulare* Subzone, 1.6 km west of Newcastle in the NW¼ sec. 31, T. 45 N, R. 61 W, Weston County, Wyoming, and from USGS Mesozoic locality D9896, limestone concretions about 18.3 m below the Turner Sandy Member of the Carlile Shale, middle Turonian *Collignoniceras woollgari* Zone, *regulare* Subzone, NW¼ sec. 35, T. 46 N, R. 63 W, Weston County, Wyoming. We have several hundred

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Fig. 38. *Collignoniceras jorgenseni* n. sp. BHI 2102, mass occurrence slab, with associated *Scaphites patulus* and *Inoceramus* sp. Carlile Shale, *C. praecox* Zone, center of sec. 35, T 8S, R 1E, Fall River County, South Dakota. Figure is ×1.

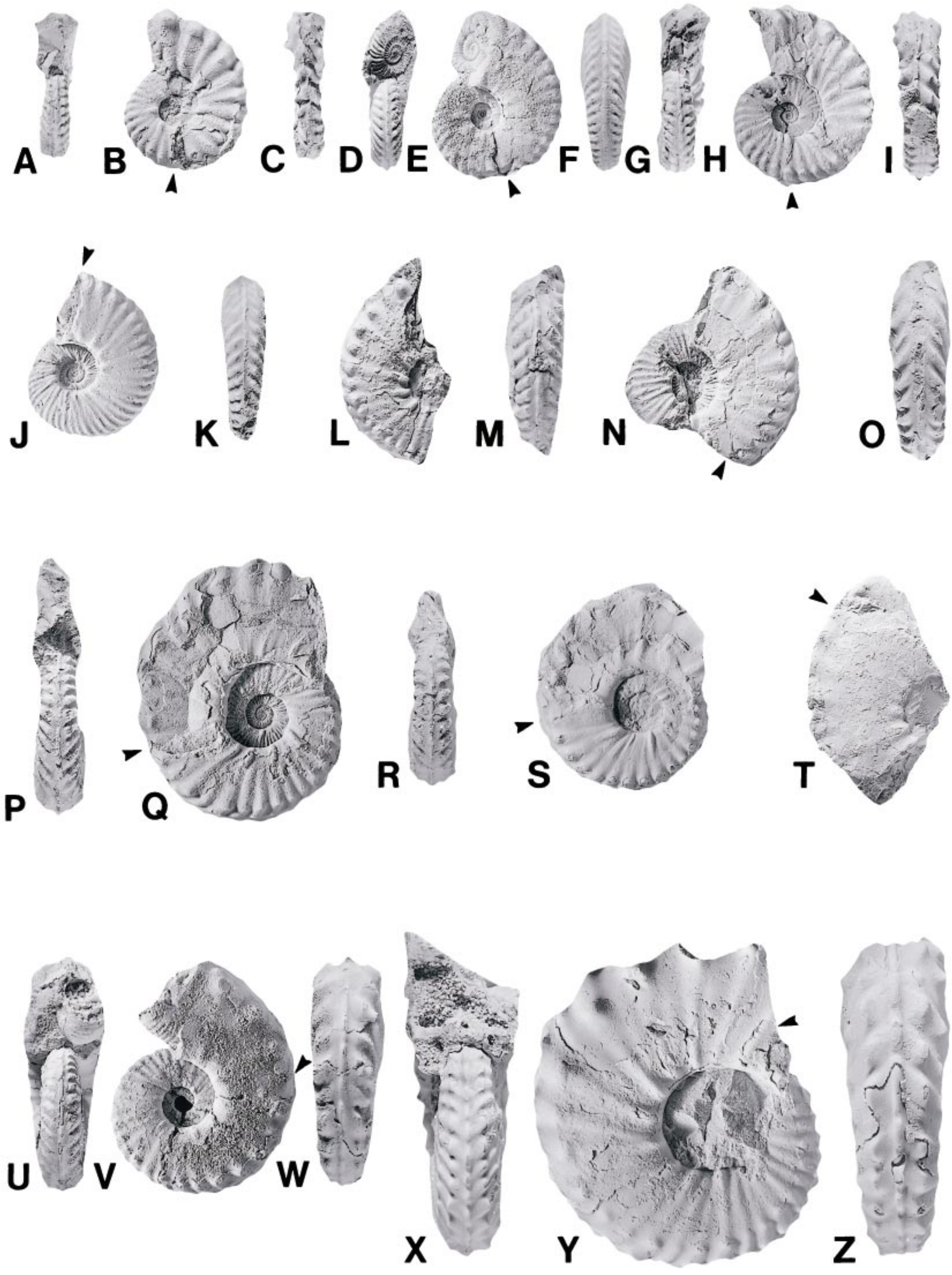

Fig. 39. *Collignoniceras praecox* (Haas, 1946), gracile form. **A–C**. USNM 498268; **D–F**. USNM 498260; **G–I**. USNM 498262; **J, K**. USNM 498259; **L, M**. USNM 498269; **N, O**. USNM 498270; **P,**

additional specimens from many localities in South Dakota, Wyoming, Colorado, Utah, and New Mexico.

DIAGNOSIS: A moderately evolute subspecies that usually has prorsiradiate single ribs that support umbilical and inner and outer ventrolateral tubercles matched by prominent siphonal clavi.

DESCRIPTION: Nuclei are highly variable (figs. 17, 21). At one extreme are compressed, high-whorled individuals of the gracile form (fig. 17A–C, J, K, O–Q, T, U, X, Y) with costal whorl breadth to height ratios of as little as 0.51 and an umbilical to shell diameter ratio of 0.29 (table 2). The umbilicus is broad, with a low umbilical wall, and a broadly rounded umbilical shoulder. The flanks are flattened and subparallel with the ventrolateral shoulders rounded. At diameters up to a maximum of 27 mm, there are dense, crowded ribs that total as many as 70 per whorl. They arise singly or in pairs at the umbilical shoulder or intercalate, arising at various levels just outside the umbilical shoulder and well below midflank. The ribs are straight, narrow and rounded, and prorsiradiate to the ventrolateral shoulder, where they flex forward; they are concave over the shoulder and project forward to the siphonal keel, producing an acute chevron. Small outer ventrolateral clavi are present from the earliest ornamented stage, and are separated by a ventral groove from the siphonal keel, which bears small clavi, equal in number to but displaced slightly aperturally of the outer ventrolateral clavi. Weaker inner ventrolateral clavi appear after the outer ones, and may be absent to a diameter of as much as 12 mm.

At the other extreme are more robust nuclei (fig. 21C, D, J–L) with whorl breadth to height ratios of up to 0.95 and an umbilical to shell diameter ratio of up to 0.40 (table 2). These have as few as 24 ribs per whorl, all of which are coarse, blunt, straight and prorsiradiate. The ribs bear weak umbilical bullae and prominent conical inner ventrolateral and clavate outer ventrolateral tubercles from an early stage. The siphonal keel is coarse.

There is every intermediate between these two forms in terms of rib density, and great variation in the diameter to which the simply ornamented stage persists. Thus, at a diameter of as little as 7 mm (fig. 21M–O) to a diameter of up to 27 mm there is a marked change in rib density; compressed gracile individuals may have as few as 17 or 18 ribs per whorl at diameters of 20–35 mm (fig. 21X–Z), decreasing to as few as 11 by a diameter of 75 mm (fig. 21U–W). The coiling in these gracile specimens is very evolute, with U/D up to 0.38 and intercostal whorl breadth to height ratios of as little as 0.57 (table 2). The umbilicus is very shallow, with a low umbilical wall, and rounded umbilical shoulder. The flanks are flattened and subparallel in intercostal section with rounded ventrolateral shoulders, and a high, sharp keel. The ribs are very narrow, and the interspaces between them become progressively wider as the diameter increases. At small diameters, the ribs originate at umbilical bullae, but with increasing diameter, the ribs become very high and flared, reaching their maximum elevation across the flanks. The ribs are markedly prorsiradiate, straight, and feebly concave across the flanks, and each rib bears a strong conical inner ventrolateral tubercle and a strong clavate outer ventrolateral tubercle. The two tubercles progressively assimilate into a flared ventrolateral rib that sweeps forward over the ventrolateral shoulder before weakening abruptly prior to meeting the siphonal keel. The keel is high and crenulate, with long, high, siphonal clavi that are markedly asymmetric in profile (fig. 23A–E). Fine lirae are developed, or not, on the interspaces between ribs (fig. 23), but do not bear any tubercles. There are an equal number of umbilical bullae, inner and outer ventrolateral, and siphonal tubercles. The largest individual of the gracile type from the Carlile Shale concretions has a diameter of 105 mm; fragments have whorl heights of up to 150 mm.

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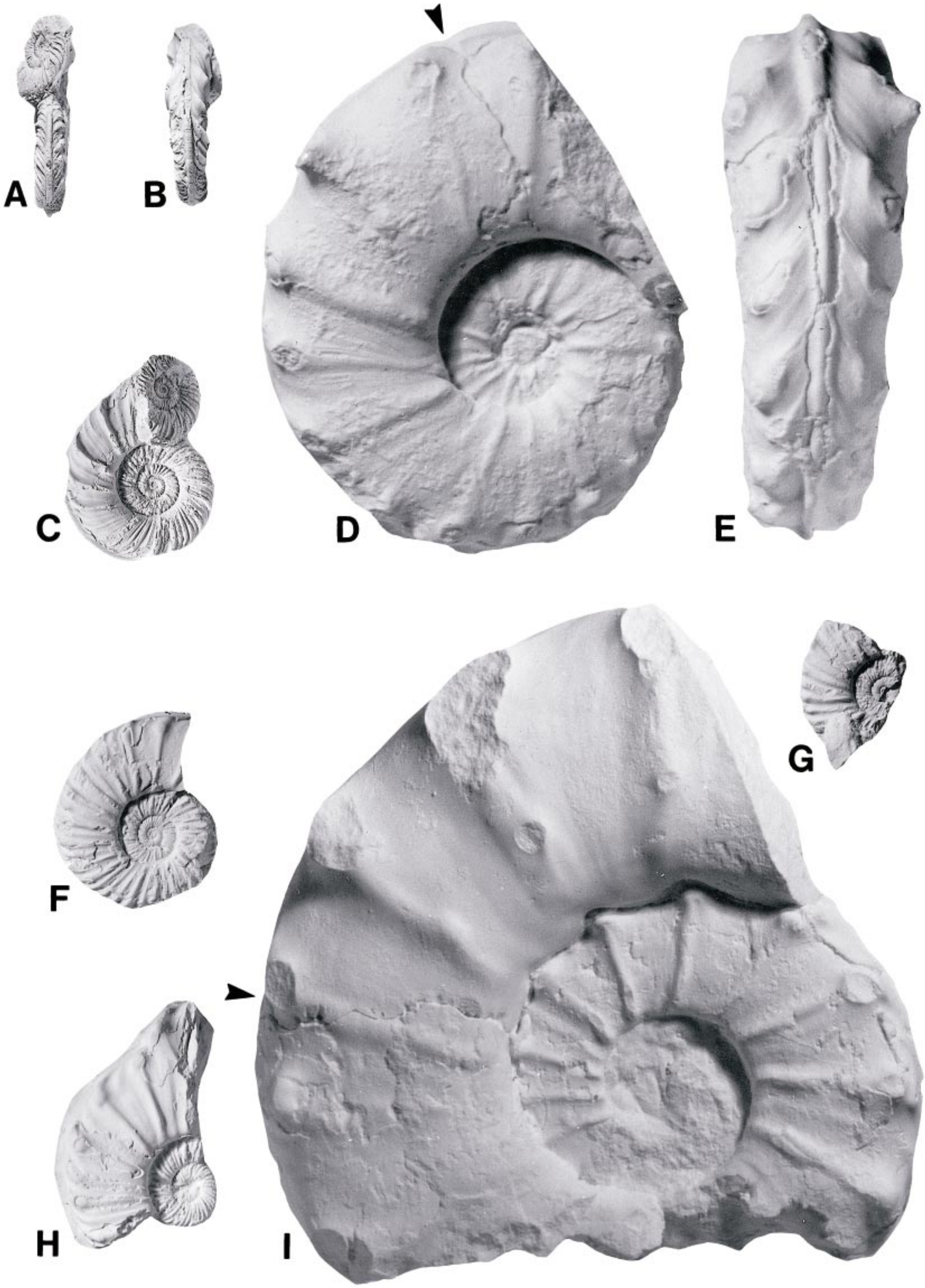
Q. USNM 498264; **R, S**. USNM 498261; **T**. USNM 498271; **U–W**. USNM 498265; all from locality 15. **X–Z**. USNM 498272 from locality 12. All figures are ×1.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Robust variants show a comparable change in ribbing density at variable diameters. At diameters of up to 75 mm, these specimens have umbilical to shell diameter ratios of up to 0.34 and a quadrate whorl section. Ribs number as few as 14 per whorl with strong, persistent umbilical bullae. Ribs are blunt, low, coarse, and prorsiradiate, and bear large, conical inner ventrolateral tubercles that are connected by broad prorsiradiate ribs to strong, outer ventrolateral clavi. The siphonal keel is coarse with clavi that correspond in number to that of the outer ventrolateral clavi. The largest observed individual of the robust type is USNM 252804, 145 mm in diameter (Cobban and Hook, 1979; pl. 3, figs. 13, 14). Other fragments are still septate at 65 mm whorl height.

The collections also contain fragments of body chambers that show distant ribs with bullae that have migrated out to an inner flank position, and enlargement of the inner ventrolateral tubercles into long, finger-like horns (fig. 20B–D), into which the outer ventrolateral clavi are progressively assimilated. The mature body chamber morphology of the gracile form is best shown by specimens from the Chispa Summit Formation at Chispa Summit in Jeff Davis County, Trans-Pecos Texas. Here, compressed adult body chambers (Kennedy et al., 1989: fig. 23) that overlap in size and ornament with the similarly compressed juveniles from the Carlile Shale of Wyoming already described reach diameters of up to 200 mm. The intercostal whorl section is compressed oval. Distant ribs bear flared umbilical bullae, which progressively migrate out from the umbilical shoulder; each ventrolateral horn is linked by a high rib to a siphonal clavus. The costal whorl section is markedly fastigiate and a low siphonal ridge links the clavi. The final portion of the body chamber before the adult aperture is smooth and tubular without major ribs, but sometimes bears nontuberculate lirae. We tentatively interpret these forms as adult microconchs.

Much larger body chambers (figs. 24, 25) belong to the robust form. A South Dakota example is shown in fig. 25; at Chispa Summit, such specimens (fig. 24) are up to 360 mm in diameter. These correspond to the robust juveniles in the South Dakota fauna and we tentatively interpret them as macroconchs. In some there is a long, low siphonal clavus corresponding to each ventrolateral horn, successive clavi being linked by a siphonal ridge. Low riblets arise from the adapical and adapertural terminations of each ventrolateral horn and loop to the siphonal clavus. In others, small siphonal clavi may be present in the interspaces between larger ones.

European specimens referred to *C. woollgari regulare* (figs. 26–32) reach comparable sizes and show the same ontogenetic changes as the U.S. material described here.

Sutures moderately incised with broad, bifid E/L, narrower L, and L/U_2 broader than U_2 (fig. 33). Several sutures were illustrated by Meek (1876a: pl. 7, fig. 1e, h) and Matsumoto (1965: fig. 6A, D, F).

DISCUSSION: Gracile microconchs and robust macroconchs can be recognized from an early ontogenetic stage; the former dominate the Black Hills assemblages upon which the above description is largely based. Haas (1946) analyzed variation in *C. woollgari*, in large part on the basis of 325 specimens from a single concretion he believed to have been collected by the Powell Survey from southern Utah. We have never seen such concretion preservation from Utah and suspect rather that the material is from the Black Hills. Haas's *Forma typica* (1946: pl. 13, figs. 1, 4–19; text-figs. 3–5, 25–29, 31–38) are macroconch fragments; the original of his plate 14, figure 11, seems to be a crushed *Plesiacanthoceras wyomingense* Reagan, 1924. Variety *regularis*, the name selected for the late subspecies of *woollgari* (Haas, 1946: 154, pl.

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Fig. 40. *Collignoniceras praecox* (Haas, 1946). **A–C**. USNM 498273, gracile form from locality 11; **D, E**. Cast of holotype, USNM 318219 (formerly 103913), robust form; **F**. Cast of paratype USNM 103913d, gracile form; **G**. Cast of paratype USNM 103913a; **H**. Cast of paratype USNM 103913b, gracile form; **I**. Cast of paratype USNM 103913e, robust form, all from the Carlile Shale, *C. praecox* Zone, at USGS Mesozoic locality 18872, 3.2 km southeast of Fairburn, Custer County, Wyoming. All figures are ×1.

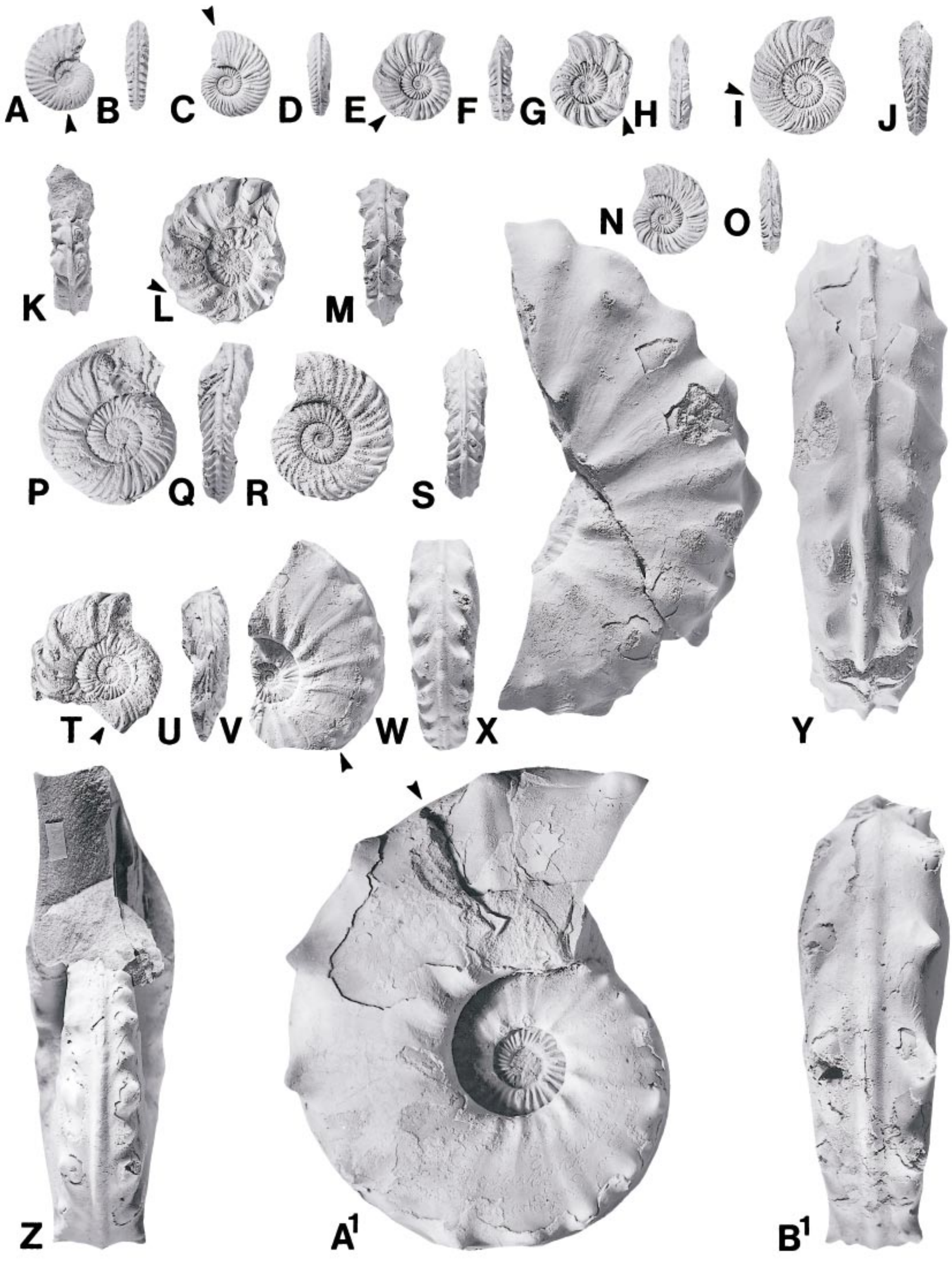


Fig. 41. *Collignoniceras praecox* (Haas, 1946), gracile form. **A, B**. USNM 498257; **C, D**. USNM 498256; **E, F**. USNM 498274; **G, H**. USNM 498275; **I, J**. USNM 498276; **K–M**. USNM 498277; **N, O**. USNM 498278; **P, Q**. USNM 498279; **R, S**. USNM 498280, **T, U**. USNM 498281; **V, W**. USNM

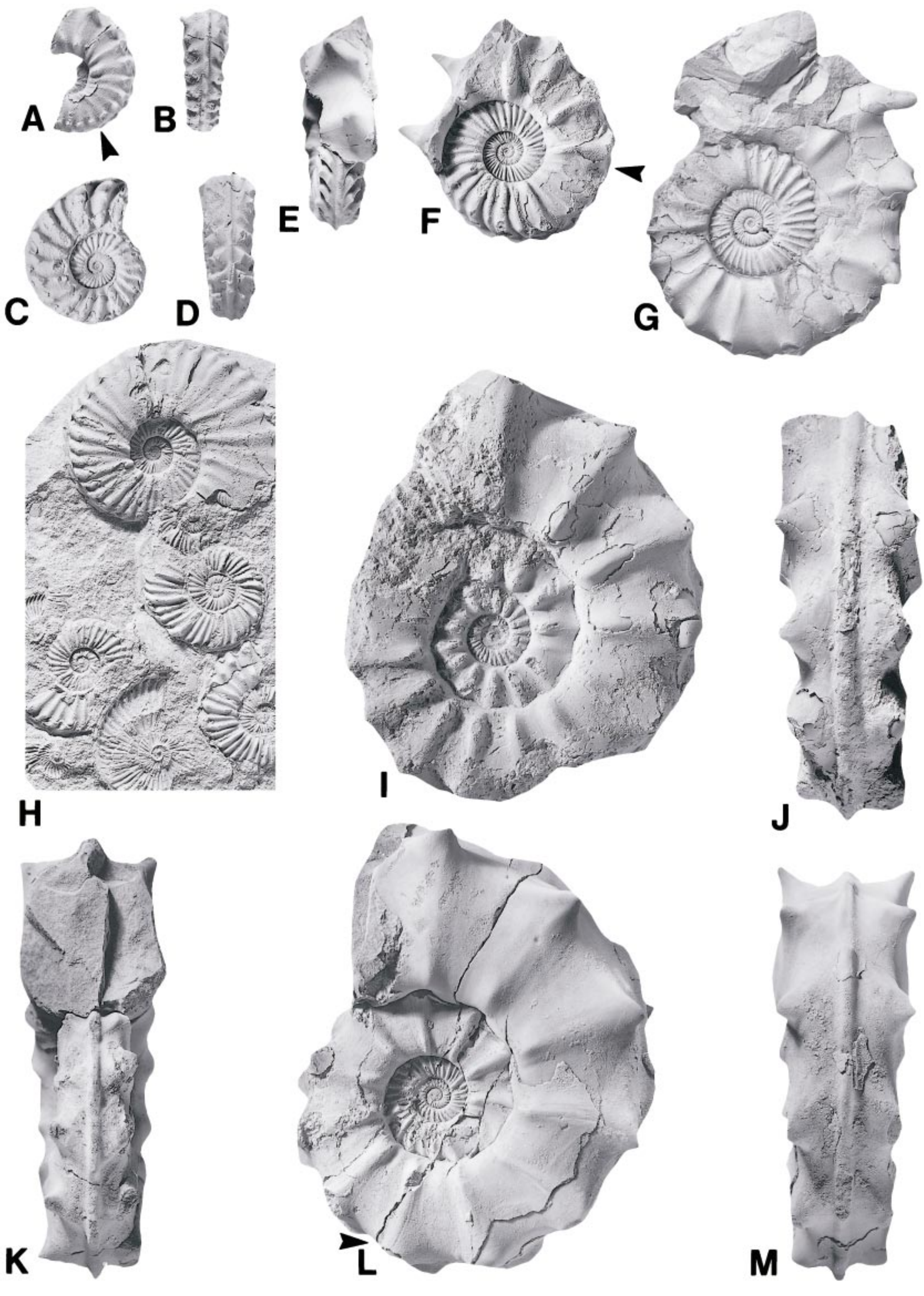
Fig. 42. *Collignoniceras praecox* (Haas, 1946), gracile form. USNM 498267 from locality 15. Figures are ×1.

16, figs. 1–17; text-figs. 10–12, 59–74, 78, 80, 81, 83), is based on gracile juvenile microconchs. Variety *crassa* (Haas, 1946: 153, pl. 14, figs. 1, 5; pl. 15, figs. 7, 8; text-figs. 6, 39) is based on evolute, robust, juvenile microconchs. Variety *intermedia* (Haas: 1946: 154, pl. 14, figs. 2–4, 6–10, 12–16; pl. 15, figs. 1–6, 9, 10; text-figs. 7–9, 40–44, 46–58) and variety *tenuicostata* (Haas, 1946: 155, pl. 16, figs. 18–21; text-figs. 13, 14, 75–77, 82) are based on juvenile microconchs.

C. woollgari var. *praecox* of Haas (1946: 155, pl. 16; figs. 2–33: pl. 17, figs. 1–5; pl. 18, figs. 1, 8, 9; text-figs. 15–18, 79, 84–90)

←

498282, all from locality 15. **X, Y**. USNM 498283, from locality 12. **Z–B¹**. USNM 498284 from locality 19. All figures are ×1.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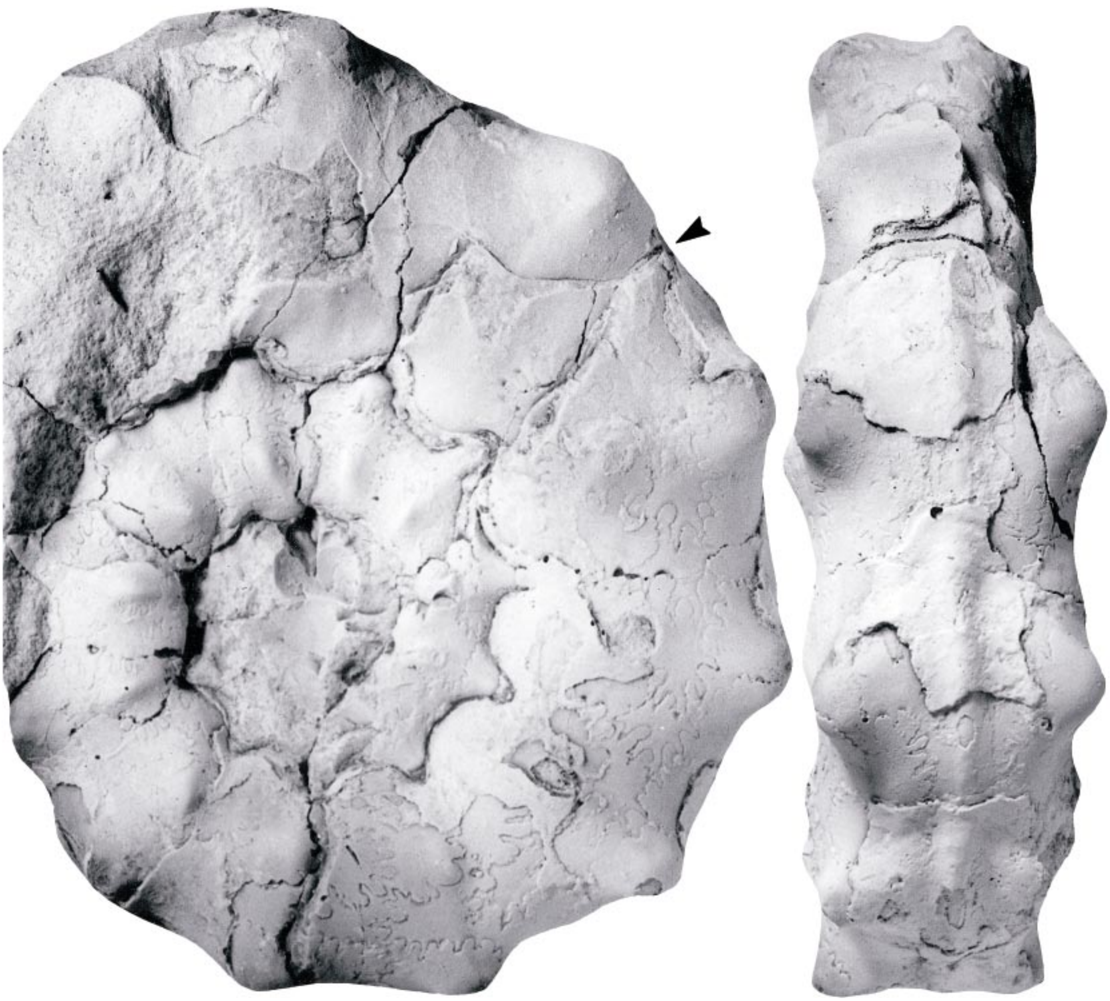

Fig. 44. *Collignoniceras praecox* (Haas, 1946), robust form. S. Jorgensen Collection, no. Co1087A, from 6–9 m (20–30 ft) below base of Turner Sandy Member, SW¼ sec. 25, T. 7S, R. 6E, Fall River County, South Dakota. Figures are ×1.

is based on specimens from USGS localities 12642 and 18872 in the Black Hills of South Dakota, and Haas specifically noted that the variety is unknown from any other locality in the Black Hills area or in the block from ''southern Utah'' that yielded specimens of his other varieties. As already noted, subsequent collecting shows that this form, here regarded as a fully separate species (*C. praecox*), is younger than *C. woollgari regulare. Collignoniceras praecox* differs in the marked differentiation of ribs into strong and

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Fig. 43. *Collignoniceras praecox* (Haas, 1946). **A, B**. USNM 498258; **C, D**. USNM 498285; **E, F**. USNM 498263, all robust forms from locality 15. **G**. S. Jorgensen Collection no. Co388A, robust form from the lower part of the Carlile Shale, sec. 25, T. 7S, R. 6E, Fall River County, South Dakota. **H**. USNM 498286, gracile forms from locality 14. **I, J**. USNM 299167, robust form from locality 21. **K–M**. USNM 498266, robust form from locality 15. All figures are ×1.

Fig. 45. *Collignoniceras praecox* (Haas, 1946), robust form. BHI 2101, Carlile Shale, *C. praecox* Zone, center of sec. 35, T. 8S, R. 1E, Fall River County, South Dakota. Figure is ×1.

bullate and weak and nonbullate in the earliest stages of development, persistence of differentiated ribbing through middle growth, and the development in the adult of inner ventrolateral bullae or spines on distant primary ribs, many ventrolateral riblets, and an entire or minutely crenulate keel.

Matsumoto (1965: 11) also analyzed variation in juvenile *Collignoniceras woollgari regulare* from a collection made from 10 m

Fig. 46. *Collignoniceras praecox* (Haas, 1946), robust form. BHI 2101, Carlile Shale, *C. praecox* Zone, center of sec. 35, T. 8S, R. 1E, Fall River County, South Dakota. Figure is ×1.

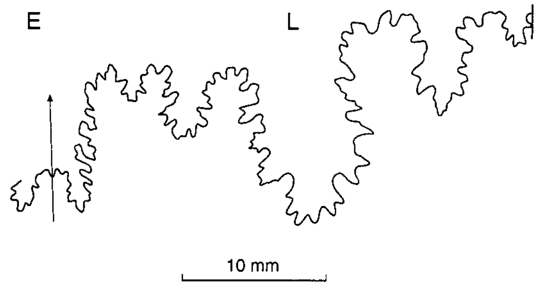

Fig. 47. *Collignoniceras praecox* (Haas, 1946). External suture of paratype USNM 103913e, copy of Haas, 1946, fig. 87. Specimen is from the Middle Turonian *C. praecox* Zone, lower part of Carlile Shale, USGS Mesozoic locality 18872, near Fairburn, South Dakota.

above the base of the Carlile Shale 3.2 mi southwest of Newcastle, Wyoming. His groups A through D and F are probably all juvenile microconchs, his group E, juvenile macroconchs.

Collignoniceras woollgari regulare differs from the nominate subspecies in that in middle and later phragmocone whorls of the latter, there are more siphonal tubercles than ventrolateral ones, and looped ribs connect opposite ventrolateral horns. This generally also separates body chambers, but multiple siphonal tubercles sometimes appear on adult body chambers of *C. woollgari regulare*, as do looped ribs.

Collignoniceras vermilionense (Meek and Hayden, 1860) (see below) is a much smaller species, showing comparable dimorphism to that of *C. woollgari regulare.* Inner whorls are coarsely ribbed. In the microconch, which is adult at 55 mm diameter, coiling is very evolute. There are only outer ventrolateral clavi whereas in *C. woollgari regulare* of this size, there are both inner and outer ventrolateral clavi.

OCCURRENCE: Widely distributed in the Western Interior of the United States from northern Montana south to Trans-Pecos Texas, and from central Utah east to western Iowa. It is also found in northeastern Texas as well as California and Oregon. The subspecies also occurs in Canada (Manitoba), northern Mexico (Chihuahua), southern England (figs. 27A–G) and France (figs. 26, 28–32).

Collignoniceras vermilionense (Meek and Hayden, 1860)

Figures 34D–H, 35A, 37 (*pars*)

Ammonites vermilionensis Meek and Hayden, 1860: 177.

Mortoniceras? *vermilionense* (Meek and Hayden). Meek, 1876a: 450, pl. 7, fig. 2.

TABLE 5
Dimensions of *Collignoniceras praecox* (Haas, 1946)[a]

Specimen	D	Wb	Wh	Wb:Wh	U
USNM 498256	14.4 (100)	4.3 (0.30)	6.5 (0.45)	0.66	4.8 (0.33)
USNM 498257	14.5 (100)	4.0 (0.28)	6.5 (0.45)	0.62	4.2 (0.29)
USNM 498258	21.0 (100)	8.2 (0.39)	9.0 (0.43)	0.91	6.4 (0.30)
USNM 498259	26.4 (100)	8.9 (0.34)	12.5 (0.47)	0.71	7.4 (0.28)
USNM 498260	27.3 (100)	8.2 (0.30)	12.4 (0.45)	0.66	6.4 (0.23)
USNM 498261	27.4 (100)	8.8 (0.32)	12.2 (0.45)	0.72	8.1 (0.30)
USNM 498262	29.3 (100)	— (—)	12.1 (0.41)	—	9.8 (0.33)
USNM 498263	31.3 (100)	12.0 (0.38)	12.7 (0.41)	0.95	10.3 (0.33)
USNM 498264	31.5 (100)	10.0 (0.31)	12.8 (0.41)	0.78	9.8 (0.31)
USNM 356918	33.3 (100)	10.4 (0.31)	13.0 (0.39)	0.80	12.0 (0.36)
USNM 498265	37.7 (100)	13.0 (0.34)	15.8 (0.42)	0.82	10.4 (0.28)
USNM 498266	76.4 (100)	25.0 (0.33)	29.3 (0.38)	0.85	27.0 (0.35)
USNM 498267	91.5 (100)	33.0 (0.36)	40.5 (0.45)	0.81	25.2 (0.28)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.

Mortoniceras vermilionense (Meek and Hayden). Stanton, 1894: 180, pl. 44, fig. 1.
Mortoniceras vermilionense (Meek and Hayden). Logan, 1898: 472, pl. 104, fig. 1.
Prionotropis vermilionensis (Meek and Hayden). Reeside, 1927: 10.
Collignoniceras vermilionense (Meek and Hayden). Cobban, 1983: 17, pl. 5, figs. 38–40 (*non* 41, 42, = *C. praecox*).
[*Collignoniceras vermilionense*]. Ludvigson et al., 1994: fig. 7a.

TYPE: Holotype by monotypy is USNM 224 (fig. 34D, E), from a limestone concretion in the Carlile Shale, inferred to be the middle Turonian *Collignoniceras praecox* Zone, on the Missouri River opposite the mouth of the Vermillion (formerly Vermilion) River in Dixon County, Nebraska.

DIAGNOSIS: A fairly small, keeled, evolute species that has closely spaced primary and secondary ribs on the innermost whorls, but mostly widely spaced, single, prorsiradiate ribs on later whorls. Ribs arise from low umbilical bullae and terminate in arcuate ventrolateral swellings that may or may not support inner ventrolateral tubercles and faint outer ventrolateral clavi. Keel is moderately high and strengthened into asymmetric clavi corresponding to the ribs.

DESCRIPTION: The holotype is a juvenile. Coiling is very evolute, with U/D = 0.44–0.46 (table 3). The umbilicus is shallow, with a low, flattened wall and broadly rounded shoulder. The flanks are flattened. There are 26 primary ribs per whorl visible at a diameter of approximately 15 mm. All arise at the umbilical seam and strengthen across the umbilical shoulder. At the smallest observed diameter, there is a slight differentiation into stronger ribs with umbilical bullae separated by somewhat weaker ribs with weak or no bullae, but this differentiation declines and disappears with increasing size, and the ribs coarsen progressively. All ribs are blunt and recti- to feebly prorsiradiate on the flanks. Each rib strengthens into an inner ventrolateral bulla from which the rib projects strongly forward, declining markedly in strength and bearing a weak outer ventrolateral clavus.

USNM 299166 (Cobban, 1983: pl. 5, figs. 39, 40; fig. 34F, G), 56.0 mm in diameter, with inner whorls that are essentially identical to those of the holotype shows the succeeding ontogenetic stages. Coiling is very evolute, with U/D = 0.46 (table 3); the umbilicus is shallow, with a low wall. The intercostal whorl section is very compressed, with a whorl breadth to height ratio of 0.63, the greatest breadth just outside the umbilical shoulder. The costal ratio is 0.76, the greatest breadth at the umbilical bulla. The inner whorls are densely and evenly ribbed with 12 primary ribs per half whorl. There are a total of 18 ribs on the outer whorl, all bullate primaries. They are narrow, very distant, prorsi-

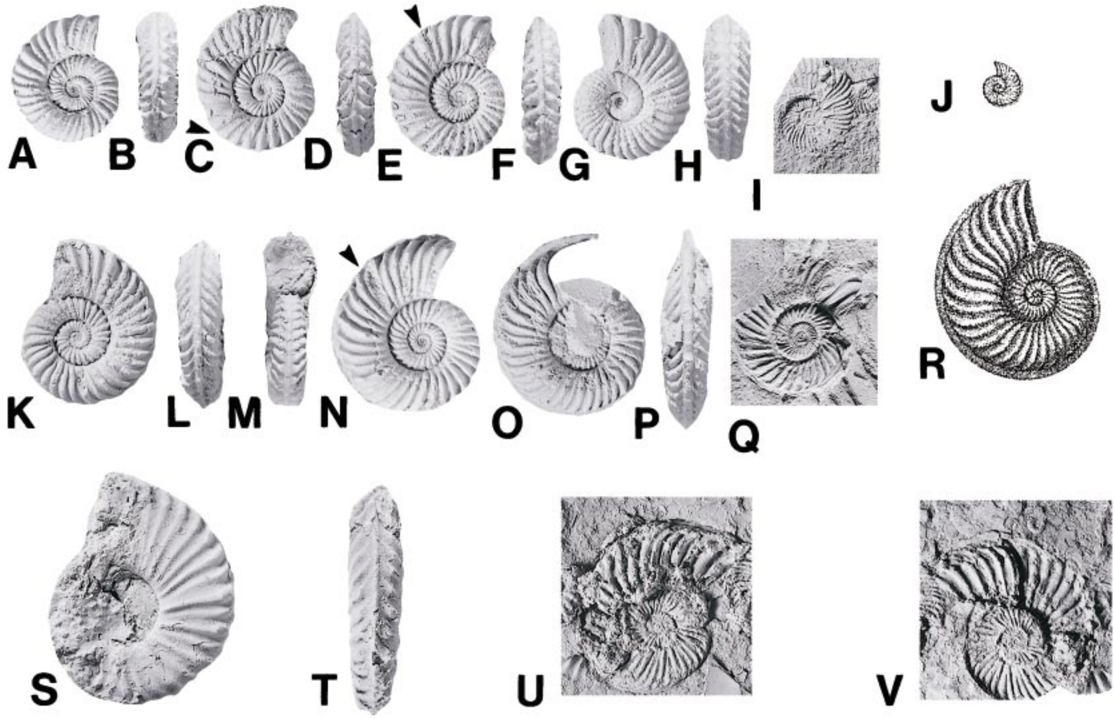

Fig. 48. *Collignoniceras percarinatum* (Hall and Meek, 1856). **A, B**. USNM 498287; **C, D**. USNM 498288; **E, F**. USNM 498289; **G, H**. USNM 498290, all from locality 15. **I**. Paralectotype AMNH 46057; **J**. Copy of Hall and Meek's original figure of AMNH 31995 (1856: pl. 4, fig. 2a). **K, L**. USNM 498291; **M, N**. USNM 498292; **O, P**. USNM 498293, all from locality 15. **Q**. Paratype AMNH 46058; **R–U, V**. lectotypes. **R** is a copy of the original figure of Hall and Meek (1856: pl. 4, fig. 2b) (AMNH 31994), **U** is AMNH 31994, and **V** is AMNH 30036, part and counterpart of the same specimen. All of the types **(I, J, Q, R, U, V)** are from rocks now assigned to the middle part of the Carlile Shale, ''Five miles below the mouth of Vermilion River on the Missouri'', that is to say, probably from the northeast side of Volcano Hill in sec. 3, T. 31N, R. 5E, Dixon County, Nebraska. **S, T**. USNM 299165 from locality 21. Figures **A–I, K–P** are ×2; fig. **J, Q–V** are ×1.

radiate to the ventrolateral shoulder, where each bears a pronounced bullate ventrolateral tubercle at the smallest diameter visible, but which thereafter declines and effaces, leaving a weakening rib that sweeps forward and is markedly concave over the ventrolateral shoulder. There is a high siphonal keel with long siphonal clavi, corresponding in number to, but displaced adaperturally of, the ventrolateral clavi or their site. The umbilical bullae decline markedly towards the aperture, suggesting that this specimen may be close to maturity.

A magnificent specimen from a limestone concretion from the Carlile Shale near Yankton, South Dakota, in the S. D. Jorgensen collection (Co1970A: fig. 34H, table 3) has one side preserved. This specimen, 83.8 mm in diameter, has a body chamber occupying the last one-half whorl and terminating in a pronounced rostrum 35 mm long. At the smallest diameter visible, approximately 7.5 mm, ribs are single and of equal height. All ribs at larger diameters are primary, narrow, and prorsiradiate. They number 32 per whorl at a diameter of about 11 mm, 26 per whorl at about 19 mm diameter, and 24 per whorl at 83 mm diameter. All arise from low, inconspicuous bullae on the narrowly rounded umbilical shoulder, incline forward on crossing the flank, rise into low bullae on the ventrolateral shoulder, and then bend forward sharply and disappear close to the keel. Bullae are reduced in size

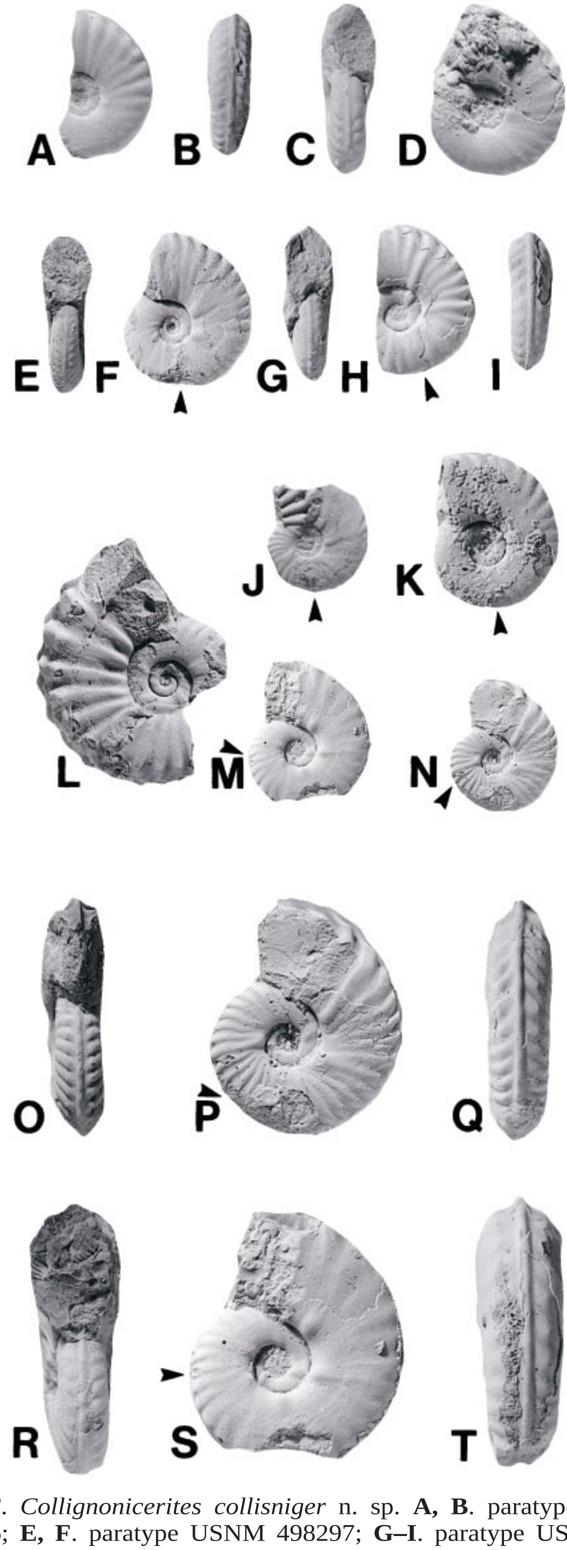

Fig. 49. **A–K, M–T**. *Collignonicerites collisniger* n. sp. **A, B**. paratype USNM 498295; **C, D**. paratype USNM 498296; **E, F**. paratype USNM 498297; **G–I**. paratype USNM 498298, **J**. paratype

TABLE 6
Dimensions of *Collignonicerites collisniger* n. gen., n. sp.[a]

Specimen	D	Wb	Wh	Wb:Wh	U
USNM 498249	17.5 (100)	5.3 (30.3)	7.0 (40.0)	0.76	4.6 (26.3)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.

near the aperture, and the last two septa are approximated.

The suture, illustrated by Meek (1876a: pl. 7, fig. 2b), is fairly simple and proportioned like that of the juvenile *Collignoniceras woollgari* figured by Meek (1876a: pl. 7, fig. 1e). Part of a suture near the aperture of the large Jorgensen specimen is shown in fig. 35A.

DISCUSSION: This is a very rare species. Cobban (1983) initially considered it *Collignoniceras praecox* (Haas, 1946). The latter, however, has straight, rectiradiate ribs that terminate in sharp horns in contrast to the prorsiradiate ribs of *C. vermilionense* that bear fowardly inclined ventrolateral bullae.

OCCURRENCE: Known only from the Carlile Shale in northeastern Nebraska and southeastern and southwestern South Dakota; *Collignoniceras praecox* Zone.

Collignoniceras jorgenseni, new species

Figures 34A–C, 35B, 36, 37 (*pars*), 38 (*pars*)

DERIVATION OF NAME: For Steven D. Jorgensen of Omaha, Nebraska, who donated the holotype and several other specimens from his extensive collections of Cretaceous ammonites.

TYPES: Holotype is USNM 498249 (fig. 36A) from the *Collignoniceras praecox* Zone in the middle Turonian Carlile Shale at USGS Mesozoic locality D13834 in the SW1/4 SW1/4 sec. 25, T. 7 S, R. 6 E, Fall River County, South Dakota. Paratypes USNM 498253 (figs. 35B, 36B–D, K) 498254 (fig. 36H–J), 498251, and 498252 are from the same locality. Paratype USNM 498250 (fig. 34A–C) is from the Carlile Shale at USGS Mesozoic locality D12683 (locality 13 in fig. 1) in the NE1/4 NW1/4 sec. 32, T. 94 N, R. 50 W, Union County, South Dakota.

DIAGNOSIS: A rather small, evolute species that has prorsiradiate primary and secondary ribs throughout. Primary ribs bear umbilical bullae and inner and outer ventrolateral tubercles. Keel supports a clavate tubercle for each rib. Primary ribs are commonly flared.

DESCRIPTION: The holotype (fig. 36A) is a small adult, 38.3 mm in diameter, embedded in part of a limestone concretion, so that only one side is visible. Slightly more than one half of the last whorl is body chamber, followed by a long rostrum. The umbilicus is shallow with U/D = 0.42 (table 4). The umbilical shoulder is narrowly rounded. Whorls are apparently higher than wide, are somewhat flattened, and have a narrowly rounded ventrolateral shoulder. The keel is fairly high and accentuated into clavi that correspond to the ribs. Those clavi corresponding to the secondary ribs are low and symmetric; those corresponding to the primary ribs are high and asymmetric with the steep slope forward.

Ornament of the holotype consists of prorsiradiate ribs of unequal heights and umbilical and ventrolateral tubercles as well as siphonal clavi. All ribs are narrow, and all arise on the umbilical shoulder. Primary ribs arise from narrow, umbilical bullae or from narrow, bullate tubercles. Each primary is inclined forward on crossing the flank and then rises into a prominent, arcuate ventrolateral swelling that supports a weak inner ventrolateral tubercle and a weaker outer ventrolat-

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USNM 498299; **K**. paratype USNM 498300; **M, R–T**. holotype, USNM 498294; **N. O–Q**. paratype USNM 498302. **L**. *Collignoniceras woollgari regulare* (Haas, 1946), robust form. All specimens are from locality 12. Figures A–L, O–T are ×2; figures M, N are ×1.

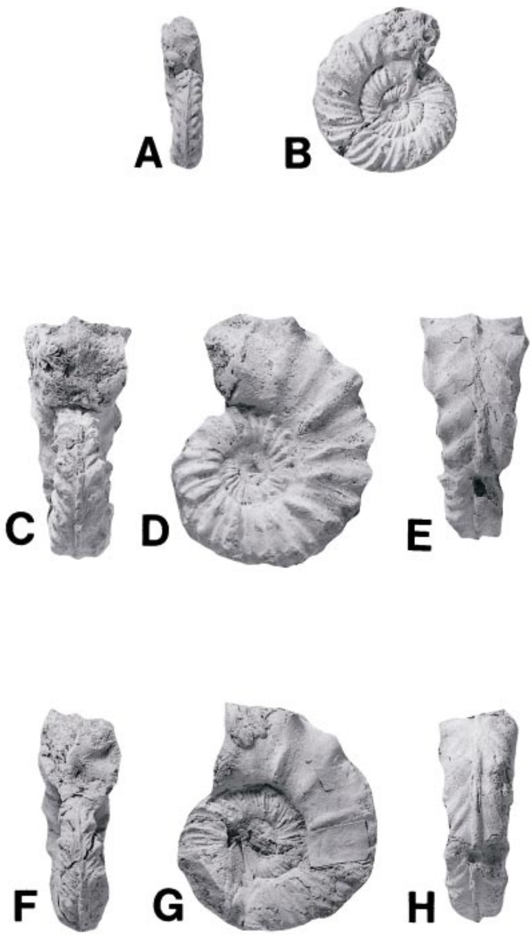

Fig. 50. *Prionocyclus hyatti* (Stanton, 1894). **A, B**. Paralectotype USNM 22941a. **C–E**. lectotype, USNM 22941. **F–H**. Paralectotype USNM 22941b. All specimens are from the Middle Turonian *P. hyatti* Zone, Codell Sandstone (Pugnellus Sandstone) of Williams Creek and Poison Canyon, Huerfano Park, Colorado. All figures are ×1.

eral tubercle before diminishing and disappearing at an acute angle to the keel. Some primaries are flared. There are 12 primaries on the outer whorl. Each pair of primary ribs is separated by one to four low, narrow, secondary ribs that are usually accentuated on the ventrolateral shoulder, but do not bear tubercles. Total primary and secondary rib counts per whorl are as follows: 35 at a diameter of approximately 6 mm, 38 at a diameter of about 14 mm, and 38 at a diameter of about 22.5 mm.

That the holotype is a small adult is revealed by the weakening and disappearance of tubercles on the last part of the body chamber, and by the presence of a long (13.5 mm) rostrum. Only short sections of the suture are visible.

Two paratypes (fig. 36B–D, K and 36H–J) from the same concretion as that of the holotype (fig. 36A) are adults 61 and 65 mm in diameter with umbilical to shell diameter ratios of 0.38 and 0.45, respectively. Both have crushed body chambers with the rostra broken off; the phragmocones are slender and probably somewhat crushed. Ribbing is sparser than that of the holotype, and primaries and secondaries alternate. Another adult paratype (unfigured) from the same concretion has a diameter of 50.5 mm and an umbilical to shell diameter ratio of 0.48. Its body chamber is also crushed, but the prominent rostrum is preserved. Most primary ribs are separated by two secondaries.

The holotype (fig. 36A) and paratypes USNM 498250 (fig. 34A–C) and 498252 represent the robust form of the species. Paratypes USNM 498253 (fig. 36B–D, K) and 498254 (figs. 36H–J) represent the gracile form.

A complete suture is not visible on any specimen. The lateral lobe and adjoining saddles on one of the paratypes is shown in fig. 35B.

DISCUSSION: *Collignoniceras jorgenseni* resembles *C. vermilionense* in size, in its wide umbilicus, and in its conspicuous prorsiradiate ribbing, but *C. jorgenseni* differs in its dense ribbing and abundant secondaries.

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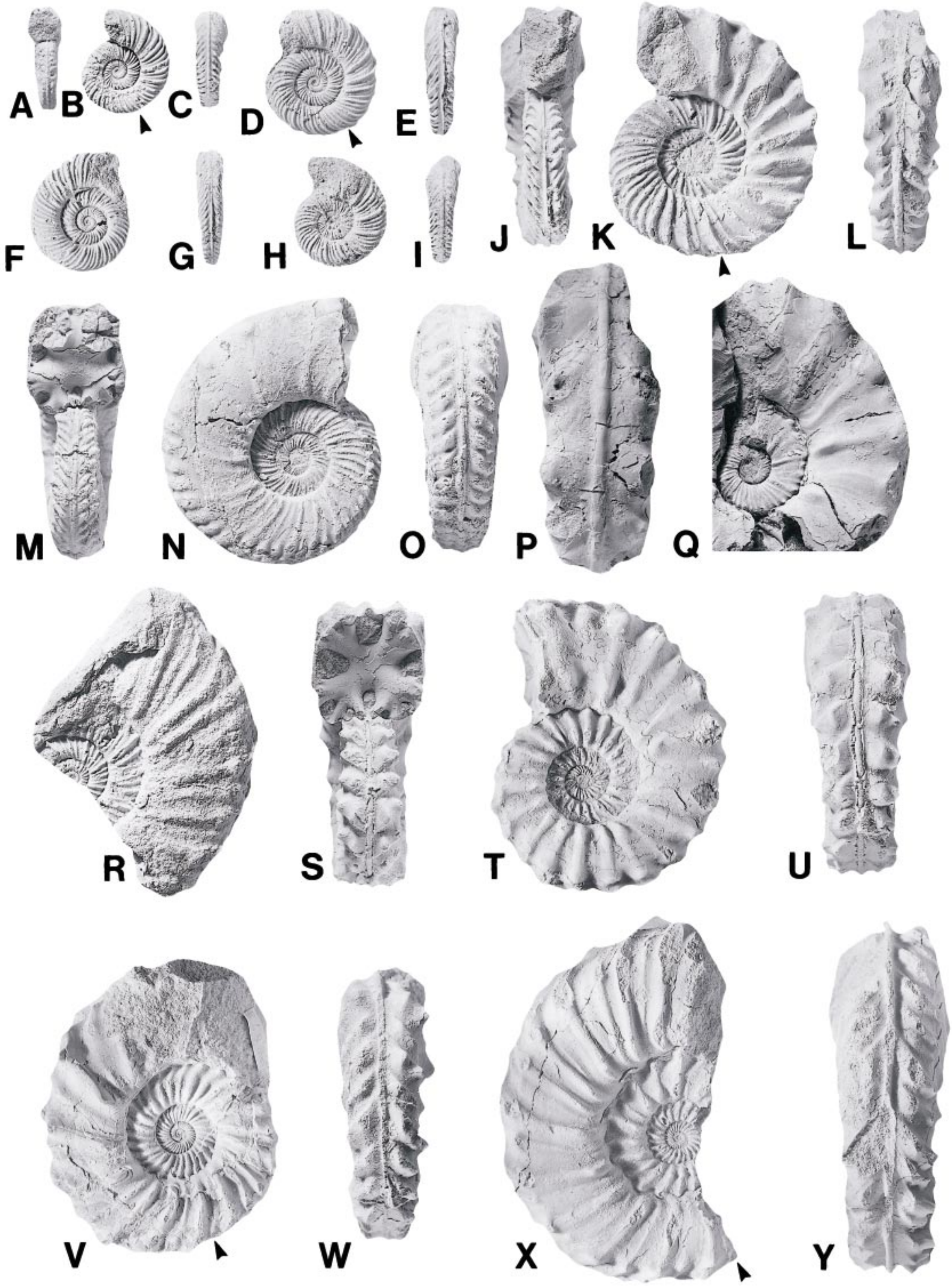
Fig. 51. *Prionocyclus hyatti* (Stanton, 1894). **A–C**. USNM 498315; **D, E**. USNM 498316; **F, G**. USNM 498303; **H, I**. USNM 498317; **J–L**. USNM 498318, all gracile forms from locality 41. **M–O**. USNM 498310, gracile form from locality 40. **P, Q**. USNM 498319, gracile form from locality 23. **R**. USNM 498320, gracile form from locality 41. **S–U**. USNM 498306, **V, W**. USNM 498321, both gracile forms, both from locality 41. **X, Y**. USNM 498311, gracile form from locality 40. All figures are ×1.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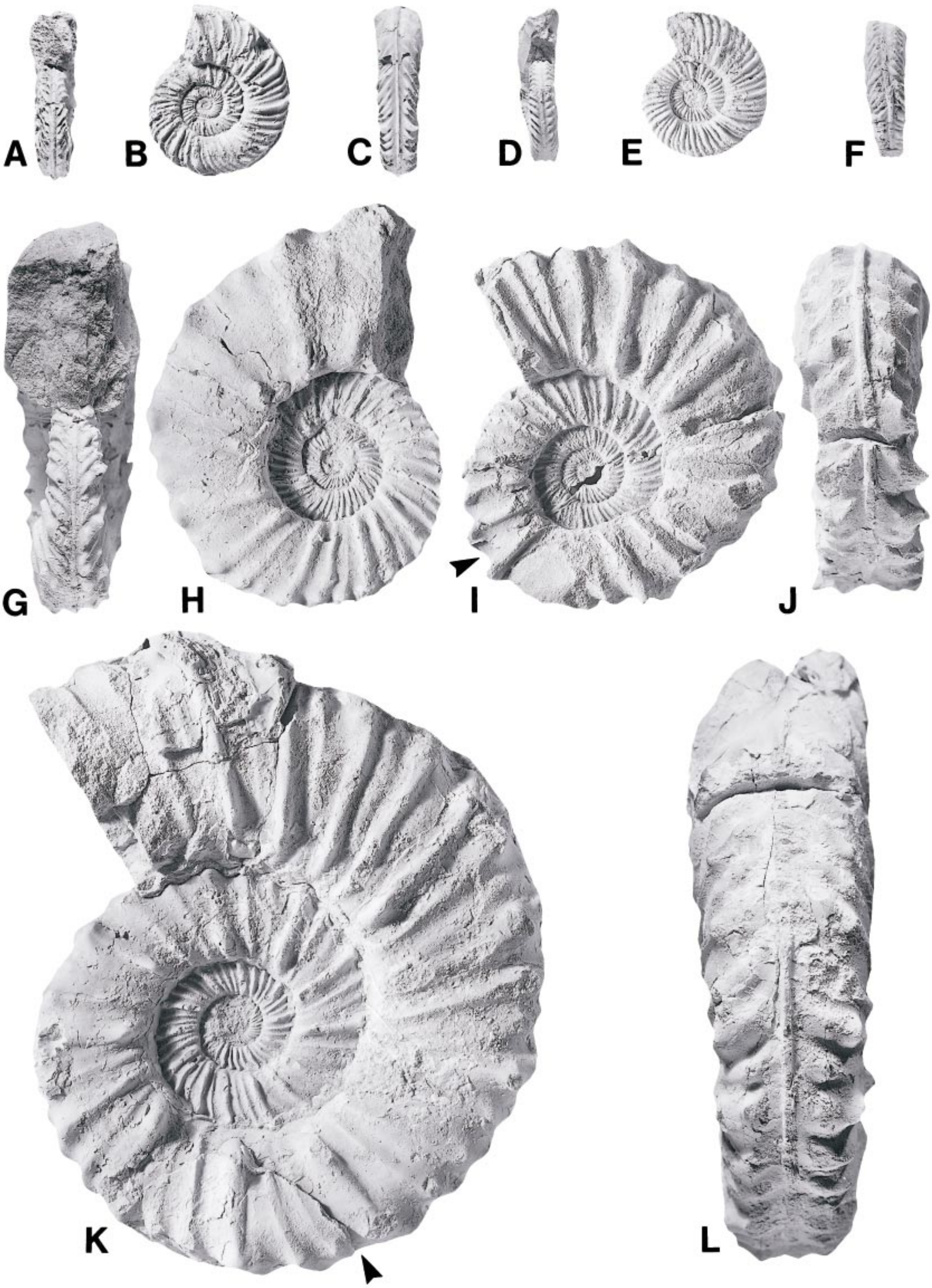
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Both forms occur with *C. praecox* and *C. percarinatum.*

OCCURRENCE: Known only from the lower part of the Carlile Shale in the Black Hills area of western South Dakota, *Collignoniceras praecox* Zone.

Collignoniceras praecox (Haas, 1946)

Figures 39–47

Prionotropis woollgari Meek (*non* Mantell) var. *praecox* Haas, 1946: 155, pl. 16, figs. 22, 23; pl. 17, figs. 1–5; pl. 18, figs. 1, 8, 9; text-figs. 15–18, 79, 84–90.

Collignoniceras vermilionense (Meek and Hayden). Cobban, 1983: 17 (*pars*), pl. 5, figs. 41, 42.

Subprionocyclus percarinatus (Hall and Meek). Cobban, 1983: 18 (*pars*), pl. 5, figs. 26–29, 32, 33, 36, 37.

Collignoniceras praecox (Haas, 1946). Reyment and Kennedy, 2001: fig. 1 k–n.

TYPES: Holotype is USNM 318219 (fig. 40D, E) (formerly 103913), paratypes USNM 103913a–e (fig. 40F–I; USNM 103913C not figured), all from the Carlile Shale, middle Turonian *Collignoniceras praecox* Zone at USGS Mesozoic locality 18872, 3.2 km southeast of Fairburn, Custer County, South Dakota.

DIAGNOSIS: Moderate to fairly large species with highly variable juvenile whorls that range from densely ribbed with distinct primaries and secondaries to more evenly and sparsly ribbed. Adults have sparser and usually weaker ribs and prominent ventrolateral horns.

DESCRIPTION: The present collections are nearly all juveniles of the gracile form. Coiling is fairly evolute, with an umbilicus to shell diameter ratio of just under 0.30 (table 5). The whorl section is compressed oval in intercostal section and polygonal in costal section with whorl breadth to height ratios of as little as 0.62. Ribbing is highly variable at small diameters (figs. 39, 40A–C, R–H; 41A–W), but generally shows a marked differentiation into strong and weak primary ribs and weak intercalaries that give these small specimens a highly distinctive appearance. There are up to 10 flared primary ribs per whorl with well-developed umbilical bullae. The primary ribs are narrow, high, and prorsiradiate on the flanks, and each bears a well-developed feebly clavate inner ventrolateral tubercle from which the rib projects sharply forward to a clavate outer ventrolateral tubercle. Between the flared primary ribs are up to four much weaker, nonbullate ribs without ventrolateral tubercles. These specimens closely match one of the paratypes (USNM 103913b, Haas, 1946: pl. 16, fig. 29, cast refigured here as fig. 40H), which shows similar ornament to a whorl height of 14 mm, at which point each weaker rib bears a feeble inner ventrolateral tubercle with pairs of both inner and outer ventrolateral tubercles present on the stronger ribs. Beyond this whorl height, the weaker ribs efface markedly, leaving primary ribs and lirae on the flanks (USNM 498283, fig. 41X, Y). In other specimens (fig. 39G–K) this stage of markedly differentiated ribs is followed, to a diameter of at least 35 mm, by a stage with crowded, dense bullate and nonbullate primary and occasional intercalated ribs that total up to 55 per whorl. These specimens are very similar to paratype USNM 103913d (Haas, 1946: pl. 18, figs. 8, 9; fig. 40F); the ribs are straight and prorsiradiate, and are separated by narrow interspaces. Each rib bears a bullate inner ventrolateral tubercle from which the rib projects abruptly forward and links to a clavate outer ventrolateral tubercle. All these variants have a pronounced siphonal keel with numerous siphonal clavi that are either as numerous or fewer in number per whorl than the ventrolateral tubercles. In middle growth there is an abrupt change to widely spaced ribs (figs. 39X–Z; 40D, E, I; 41X, Y). Bullate primaries alternate with nonbullate long and short ribs, all with conical inner and clavate outer ventrolateral tubercles, the compressed whorl section and feeble flank

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Fig. 52. *Prionocyclus hyatti* (Stanton, 1894). **A–C**. USNM 498309; **D–F**. USNM 498322; **G, H**. USNM 356904; **I, J**. USNM 498323; **K, L**. USNM 498324, all gracile forms from locality 41. All figures are ×1.

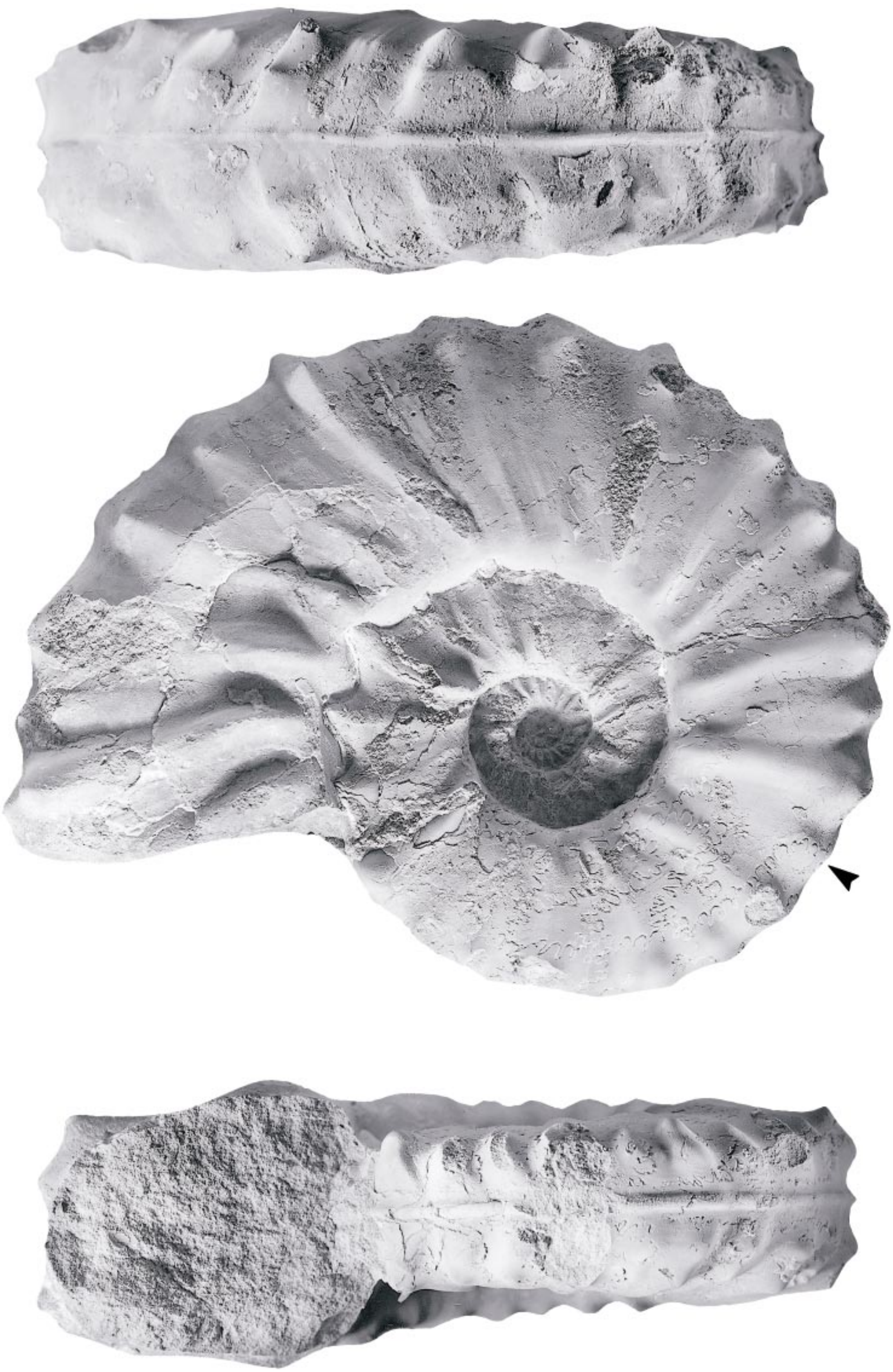

Fig. 53. *Prionocyclus hyatti* (Stanton, 1894). USNM 498312, gracile form from locality 41. All figures are ×1.

Fig. 54. *Prionocyclus hyatti* (Stanton, 1894). USNM 498325, gracile form, from locality 41. All figures are ×1.

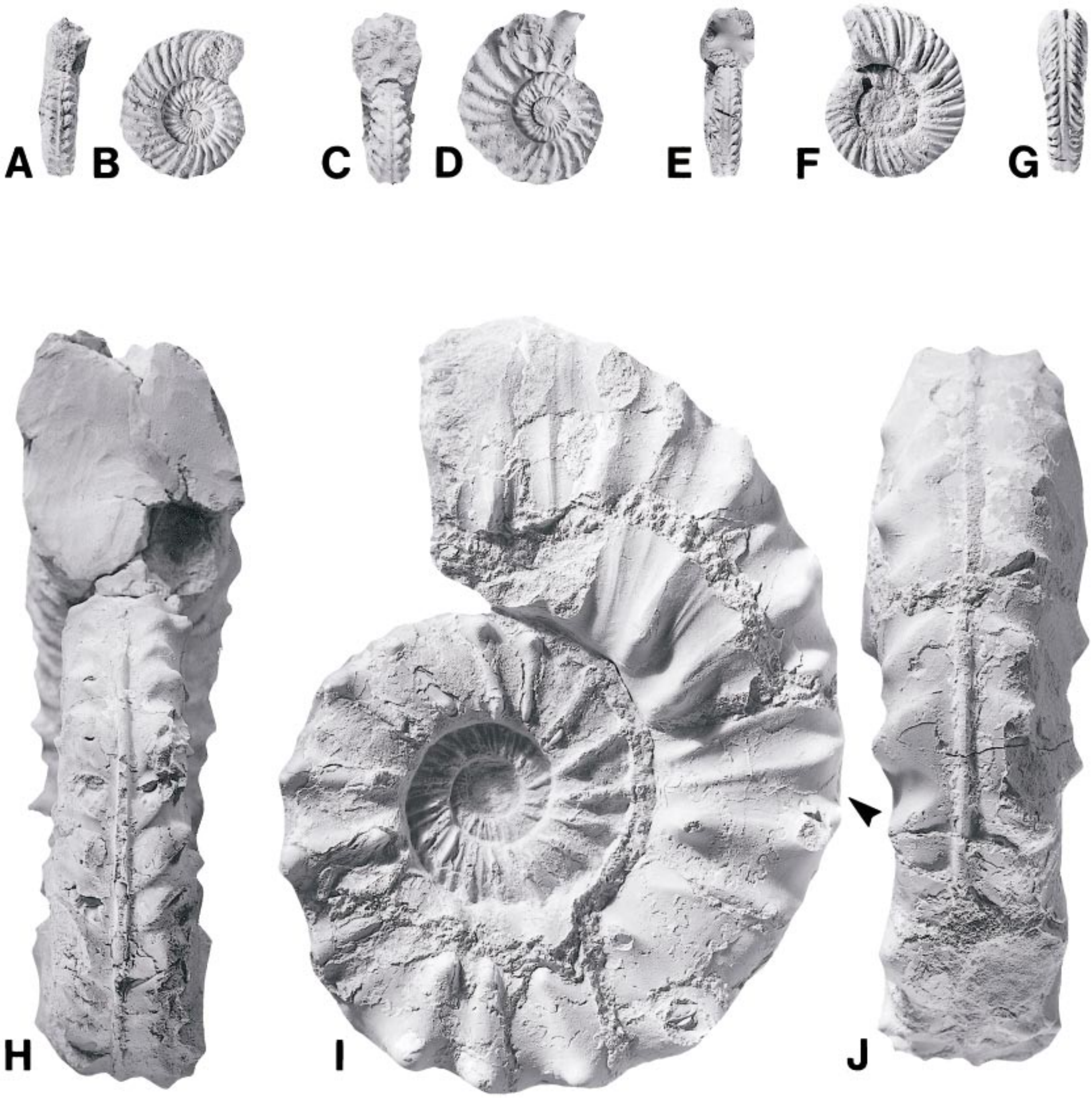

Fig. 55. *Prionocyclus hyatti* (Stanton, 1894). **A, B**. USNM 498326, gracile form from locality 41; **C, D**. USNM 498304, robust form from locality 40. **E–G**. USNM 498327, gracile form from locality 42. **H–J**. USNM 498328, gracile form from locality 41. All figures are ×1.

ornament being distinctive at this size; the holotype is just such a specimen (fig. 40D, E). In ventral view these specimens show the ribs extending in attenuated form forward to intersect the line of the keel at an acute angle, with the interspaces between ribs covered in growth striae, lirae, and riblets. At this stage, the crenulations on the keel are very sub-

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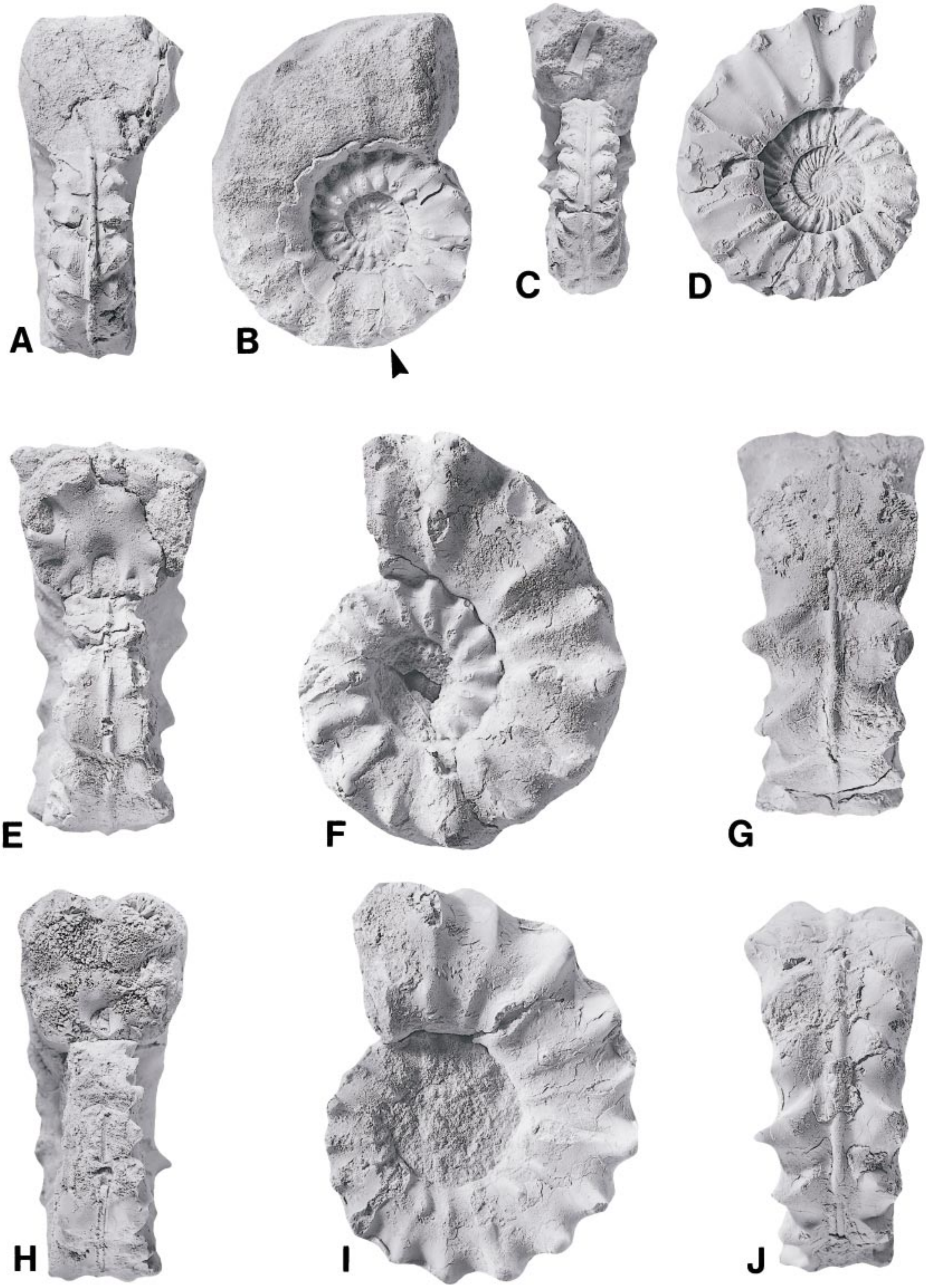
Fig. 56. *Prionocyclus hyatti* (Stanton, 1894). **A, B.** USNM 498329, robust form from locality 41. **C, D**. USNM 498305, robust form from locality 42. **E–G**. USNM 498308, robust form from locality 40. **H–J**. USNM 498307, robust form from locality 41. All figures are ×1.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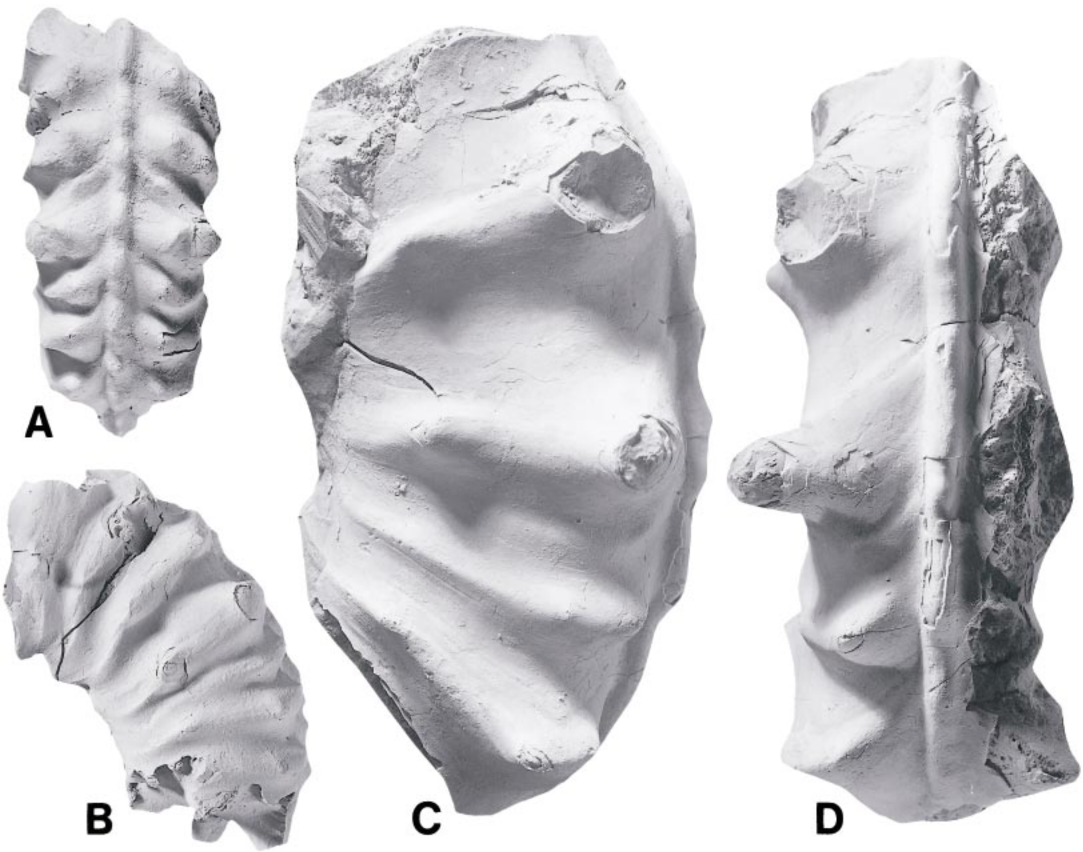

Fig. 57. *Prionocyclus hyatti* (Stanton, 1894). **A, B**. USNM 498330; **C, D**. USNM 498331, both robust forms from locality 23. All figures are ×1.

dued. In some there are merely irregular elevations; in others (e.g., Haas, 1946: pl. 17, fig. 4; fig. 40I) the keel is almost entire. Our largest specimen of this kind, USNM 498267 (fig. 42), shows progressive effacement of flank ornament and the coalescence of inner and outer ventrolateral tubercles into blunt inner ventrolateral horns. USNM 498284 (fig. 41Z–B′) shows the same transition at only 60 mm diameter.

Juveniles of the robust form are evolute with U/D up to 0.35 (fig. 43E, F; table 5). Their innermost whorls may or may not show differentiation into strong, bullate and weaker, nonbullate ribs. In middle growth, the few available specimens have strong, distant primary ribs with bullae and inner and outer ventrolateral tubercles differentiated to whorl heights of up to 30 mm, with shorter, weaker ribs between. Adults (figs. 44–46) have sparse primary ribs ending in pronounced ventrolateral tubercles or horns.

Several sutures were shown by Haas (1946: figs. 79, 84–90); that of one of the paratypes (USNM 103913e) is reproduced here (fig. 47).

DISCUSSION: Haas (1946: 156) rightly remarked on the distinctive features of this species: ‘‘the accelerated development of this variety from maturity to the latest ontogenetic stage has been alluded to in its name. The differentiation between stronger and weaker ribs and the later disappearance of those of the latter kind cause this variety, of all of the various forms of *P. woollgari*, most to resemble the genus *Prionocyclus.* Furthermore it is the only form of, or close to *P. woollgari* here dealt with that might perhaps be granted the status of an independant species.’’ *Collignoniceras praecox* thus

TABLE 7
Dimensions of *Prionocyclus hyatti* (Stanton, 1894)[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
Robust forms						
USNM 498303	Costal	21.1 (100)	5.5 (26.2)	6.8 (32.2)	0.81	9.2 (43.6)
USNM 498304	Costal	24.0 (100)	9.2 (38.3)	9.2 (38.3)	1.00	9.1 (37.9)
USNM 498305	Costal	48.9 (100)	23.0 (47.0)	16.2 (33.1)	1.42	19.6 (40.1)
	Intercostal	44.8 (100)	16.5 (36.8)	13.8 (30.8)	1.20	19.6 (43.8)
USNM 498306	Costal	51.5 (100)	18.8 (36.5)	18.0 (35.0)	1.04	19.5 (37.9)
	Intercostal	49.3 (100)	16.6 (37.8)	16.4 (33.3)	1.01	19.5 (39.6)
USNM 498307	Costal	62.0 (100)	29.8 (48.0)	22.3 (36.0)	1.34	24.2 (39.0)
	Intercostal	59.9 (100)	22.4 (37.4)	20.0 (33.4)	1.12	24.2 (40.4)
USNM 498308	Costal	70.0 (100)	34.3 (49.0)	23.5 (33.6)	1.46	26.3 (37.6)
	Intercostal	66.7 (100)	26.6 (39.9)	22.5 (33.7)	1.18	26.3 (39.4)
Gracile forms						
USNM 498309	Costal	24.0 (100)	9.0 (37.5)	9.8 (40.8)	0.92	12.0 (50.0)
USNM 498310	Costal	46.0 (100)	16.3 (35.4)	13.5 (29.3)	1.21	16.5 (35.9)
USNM 498311	Costal	61.5 (100)	21.3 (34.6)	22.4 (36.4)	0.95	24.8 (40.3)
	Intercostal	59.6 (100)	18.0 (30.2)	21.4 (35.9)	0.84	24.8 (41.6)
USNM 498312	Costal	129.0 (100)	43.0 (33.3)	47.5 (36.8)	0.91	49.5 (38.4)
	Intercostal	124.5 (100)	38.6 (31.0)	43.8 (35.2)	0.88	49.5 (40.0)

[a] See table 1 for explanation of symbols.

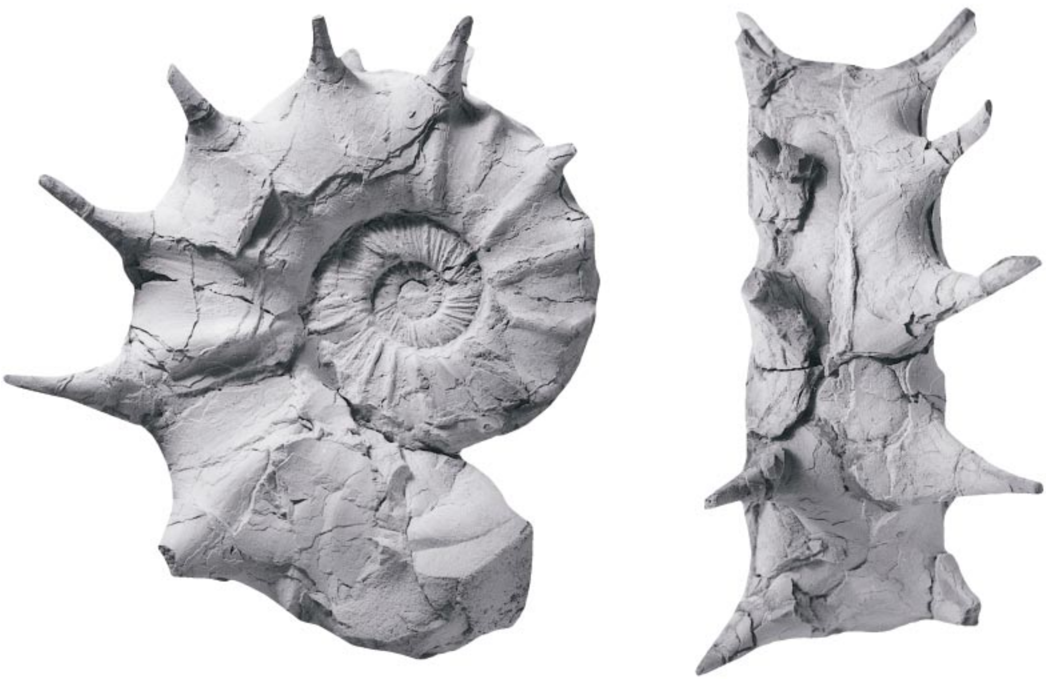

Fig. 58. *Prionocyclus hyatti* (Stanton, 1894). USNM 487697, robust form from locality 23. Figures are ×1.

Fig. 59. *Prionocyclus hyatti* (Stanton, 1894). USNM 498332, detached ventrolateral horn, from locality 23. Figures are ×1.

differs from *C. woollgari regulare* in the middle growth stages by the persistence of long and short ribs, with ventrolateral tubercles outnumbering umbilicals. The presence of a near continuous keel where *C. woollgari regulare* has clavi equal in number to the ventrolateral tubercles is also distinctive. Adult *C. woollgari* are much larger than those of *C. praecox*, and have a highly distinctive ribbing and ventral ornament. There are closer similarities between juvenile *C. woollgari woollgari* and *C. praecox*, but the strong siphonal clavi of the former, corresponding to the outer ventrolateral tubercles in number, separates them; adults are very different.

OCCURRENCE: Known with certainty only from the lower part of the middle Turonian Carlile Shale of South Dakota, *Collignoniceras praecox* Zone.

Collignoniceras percarinatum (Hall and Meek, 1856)

Figure 48

Ammonites percarinatus Hall and Meek, 1856: 396, pl. 4, fig. 2a, b.
Prionotropis woolgari (sic) Mantell (sp.). Stanton, 1894: 174.
Ammonites percarinatus Hall and Meek. Diener, 1925: 32.
Prionotropis percarinatus (Hall and Meek). Haas, 1946: 150, 158.
Collignoniceras woollgari (Mantell). Stephenson, 1953: pl. 12, fig. 3.
Subprionocyclus percarinatus (Hall and Meek). Cobban, 1983: 18, pl. 5, figs. 30, 31, 34, 35 (*non* figs. 26–29, 32, 33, 36, 37 (= *Collignoniceras praecox*)); pl. 15, figs. 5, 6.
Prionocyclus percarinatus (Hall and Meek). Cobban, 1984a: 75, 84.
non Prionocyclus percarinatus (Hall and Meek, 1856). Kirkland, 1996: 99, pl. 40, figs. B–F, I.

TYPES: Lectotype AMNH 31995 (fig. 48J), designated by Cobban (1983: 18), and paratypes are from ''Five miles below the mouth of Vermilion River on the Missouri'' (Hall and Meek, 1856: 396). As noted by Cobban (1983: 18), the specimens came from rocks now assigned to the middle Turonian Carlile Shale, probably from the northeast side of Volcano Hill in sec. 3, T. 31 N, R. 5 E, Dixon County, Nebraska.

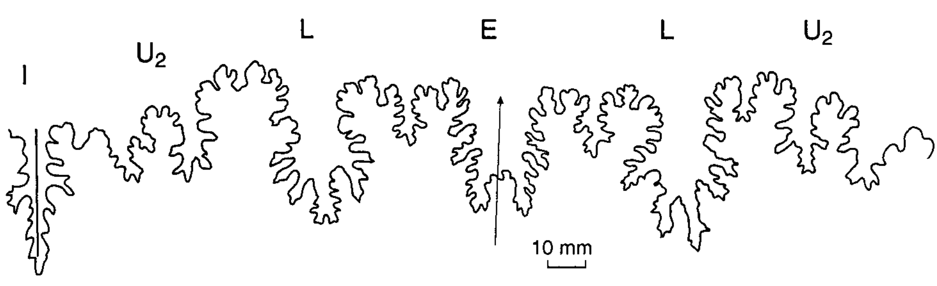

Fig. 60. Suture of *Prionocyclus hyatti* (Stanton, 1894). Copy of Haas, 1946, figure 45. The original is from the Blue Hill Member of the Carlile Shale of Kansas.

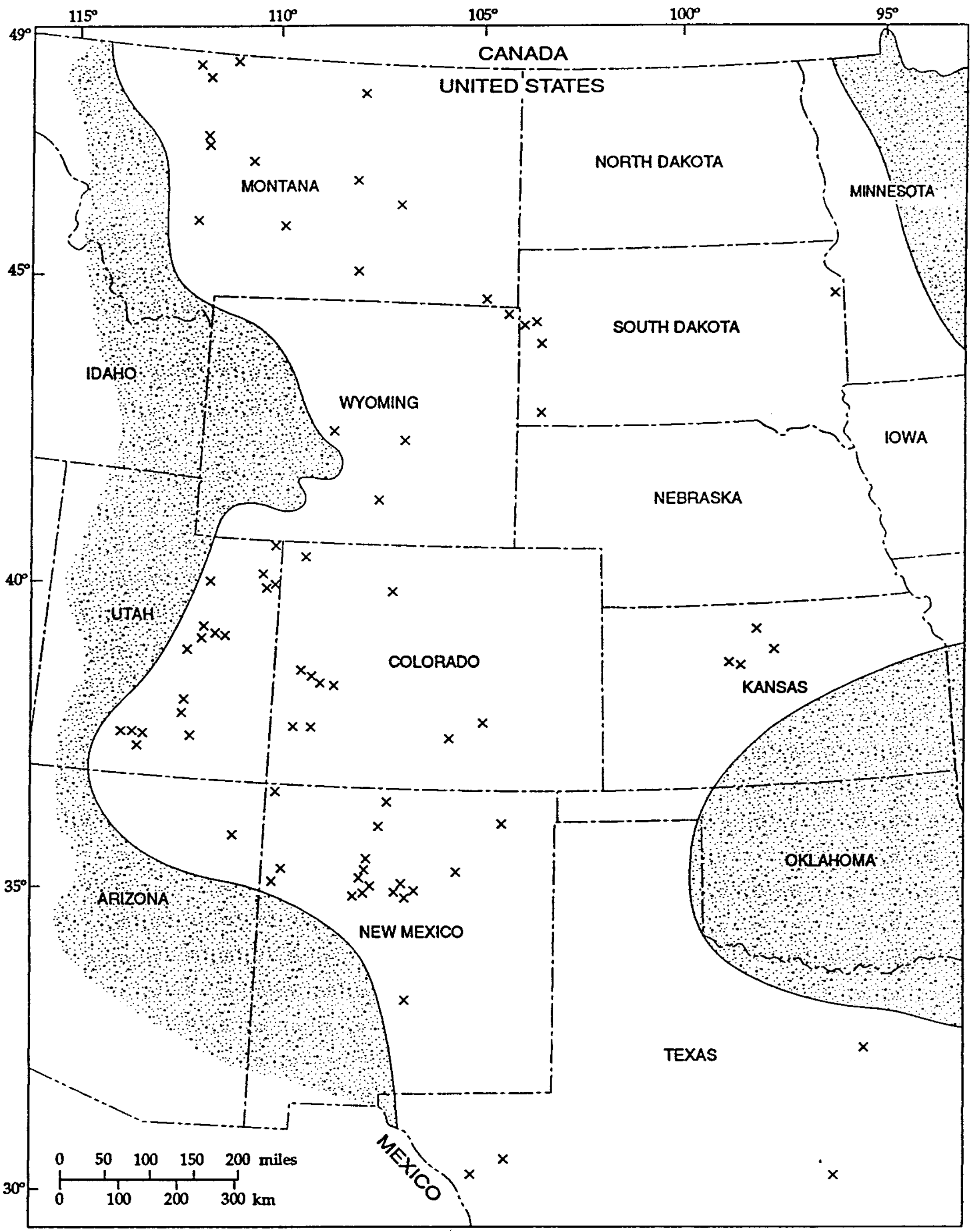

Fig. 61. Distribution of *Prionocyclus hyatti* (Stanton, 1894) in the Western Interior Seaway during the early Middle Turonian. Land areas indicated by stipple. Modified after Cobban et al. (1994).

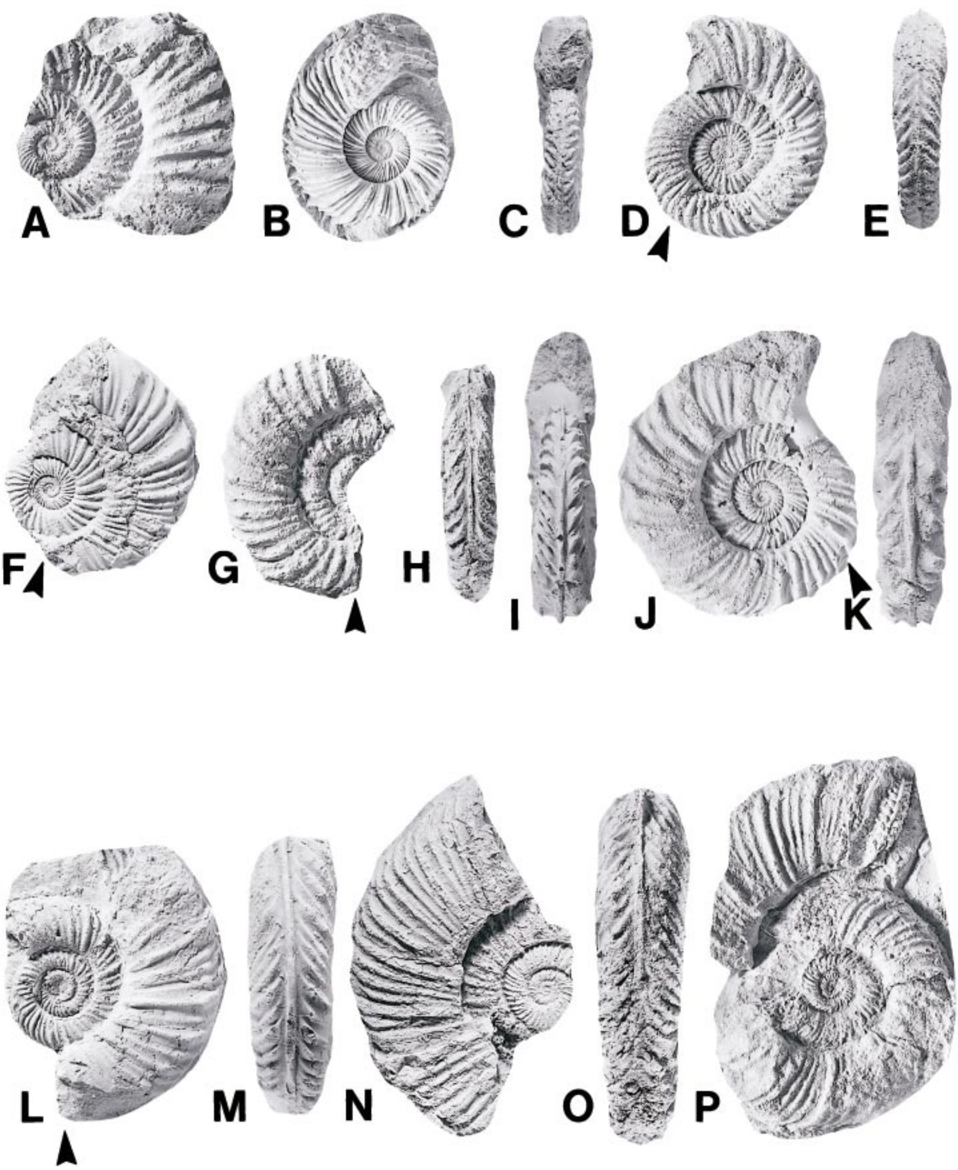

Fig. 62. *Prionocyclus albinus* (Fritsch, 1872). **A**. USNM 498333, from locality 32. **B**. USNM 220385, from locality 22. **C–E**. USNM 498334, from USGS Mesozoic locality 35. **F**. USNM 498335, from locality 63. **G, H**. USNM 498336, from locality 32. **I–K**. USNM 356899, from locality 40. **L, M**. USNM 498337, from locality 63. **N, O**. USNM 498338, from locality 32. **P**. USNM 498339, from locality 32. All figures are $\times 1$.

DIAGNOSIS: A small species that has closely spaced, prorsiradiate ribs of rather uniform height. Ribs bend forward at the ventrolateral shoulder and fade out at the low keel. Keel notched by low clavi that correspond in number to the ribs.

DESCRIPTION: Hall and Meek's description is as follows: ''Discoidal, depressed; umbilicus wide and shallow; volutions about four or five, all visible in the umbilicus, scarcely one fourth of each embraced in the succeeding one; shell thin; surface

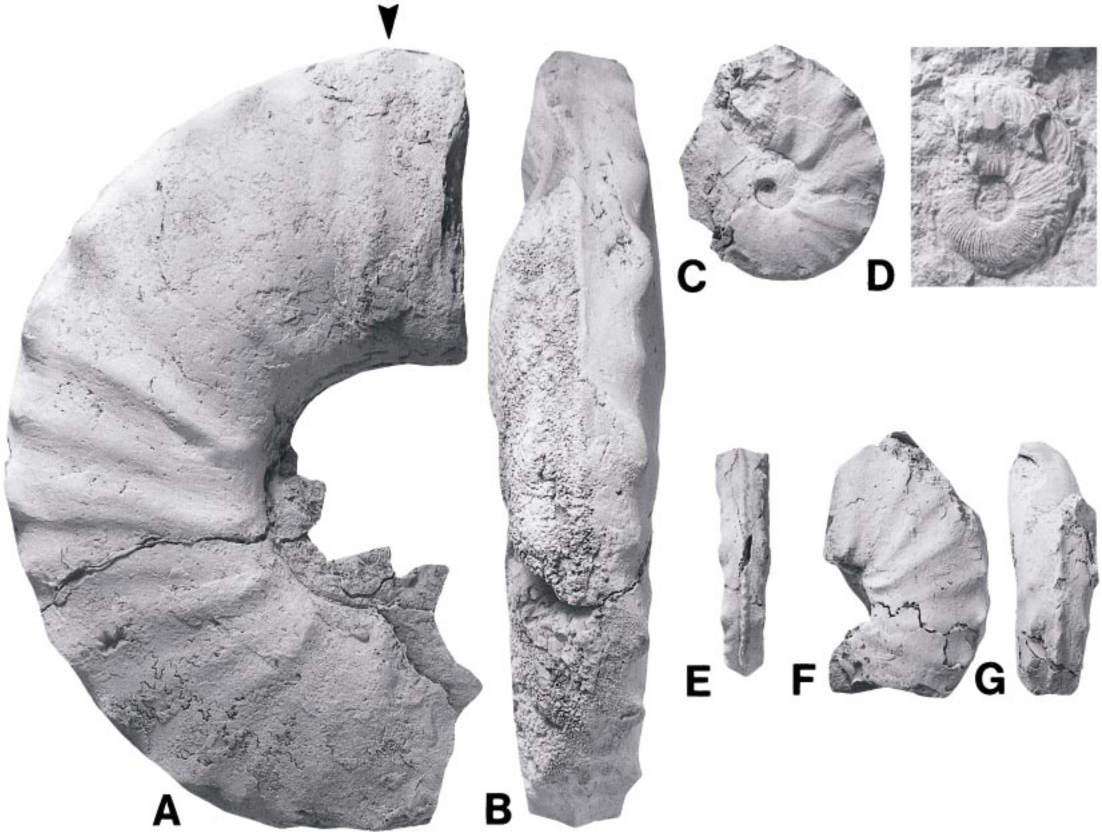

Fig. 63. *Prionocyclus macombi* Meek, 1876. **A, B**. lectotype, USNM 20259, from the Juana Lopez Member of the Carlile Shale in Colfax County, New Mexico. **C–G**. USNM 22940, the originals of Stanton, 1894, plate 41, figures 1–3, from ''near Mancos, southwestern Colorado, about 400 feet above the base of the Colorado Cretaceous shales, where it is associated with *Ostrea lugubris* and *Inoceramus dimidius*.'' Figures A–C, E–G are ×1; figure D is ×2.

marked by thirty-eight to forty-five prominent flexuous sharp ribs some of which originate in the umbilicus, and others upon the lateroventral margin, and all extend to the dorsolateral edge, where they bend abruptly forward, and terminate before reaching the dorsal line, which is marked by a thin sharp carina extending to the aperture. Ribs thickened and sometimes nodose towards the periphery. Our specimens are all casts of the interior with fragments of the shell adhering, and the condition is such as to give no means of determining the character of the septa.''

A suite of small specimens from limestone concretions in the lower part of the Carlile Shale at locality 15 in figure 1, USGS Mesozoic locality D10697, in Fall River County, South Dakota, seem assignable to this species (fig. 48A–H, K–P). The specimens are fairly evolute with umbilical to shell diameter ratios of 0.33–0.48 and 32–38 ribs on the outer whorl. Ribs are prorsiradiate, arise at the umbilicus, cross the flank, and curve forward at the ventrolateral shoulder, where they are accentuated a little or actually form low clavate tubercles. The low keel bears asymmetrical clavi that have the steeper slope on the adoral side. Each siphonal clavus matches a rib.

DISCUSSION: The presence of a siphonal clavus for each rib supports the assignment to *Collignoniceras* rather than to *Prionocyclus*. In later whorls, the species resembles *C. vermilionense* in having single prorsiradiate ribs that bend forwards sharply on the

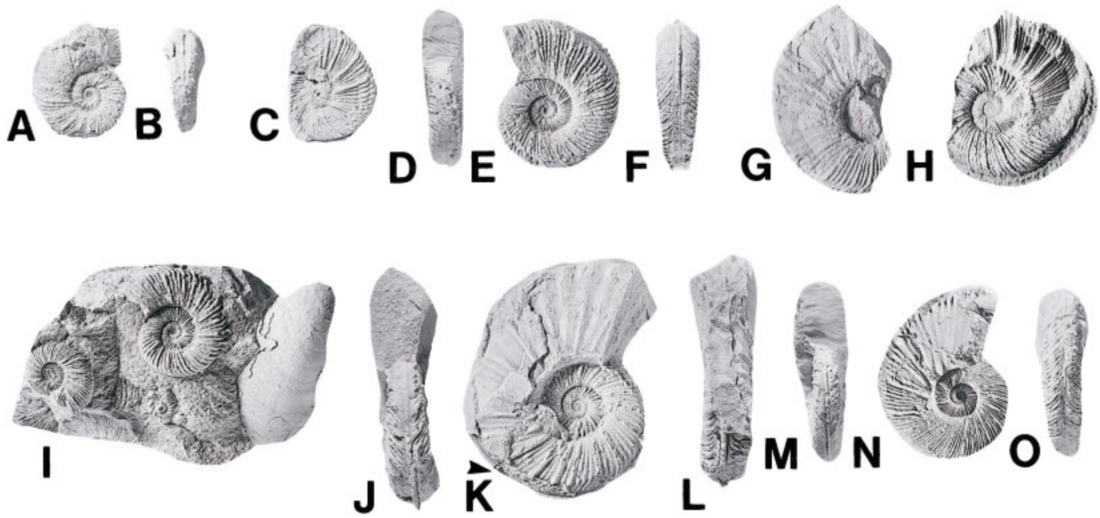

Fig. 64. *Prionocyclus macombi* Meek, 1876. **A, B**. USNM 498353; **C.** USNM 498354; **D–F**. USNM 498355; **G**. USNM 498356; **H**. USNM 498357; **I**. USNM 498358; **J–L**. USNM 498359; **M–O**. USNM 498360, all variants of the gracile form, from locality 27. All figures are ×1.

ventrolateral shoulder. The latter species, however, is much more coarsely ribbed and has larger, more pronounced siphonal clavi.

OCCURRENCE: Known only from the middle Turonian Carlile Shale, *Collignoniceras praecox* Zone, of southeastern South Dakota, northeastern Nebraska, and western Minnesota. Specimens figured as *Prionocyclus percarinatus* by Kirkland (1996: 99, pl. 40, figs. B–F, I) from the *Collignoniceras woollgari regulare* Subzone in the Mancos Shale of northeastern Arizona have differentiated ribs to a much larger size than on *C. percarinatus* and represent some other species. Likewise, specimens recorded as *Subprionocyclus percarinatus*? from the Mancos Shale of west-central New Mexico by Hook et al. (1983: sheet 1) also belong to some other species.

Genus ***Collignonicerites,*** new genus

DERIVATION OF NAME: *Collignoniceras* plus *ites* (Latin)—descendant of *Collignoniceras*.

TYPE SPECIES: *Collignonicerites collisniger* n. gen., n. sp.

DIAGNOSIS: Small, adult at 18 mm or less, involute with compressed whorl section. Distant, blunt umbilical bullae give rise to pairs or groups of ribs, with one or several nonbullate long ribs between; ribs blunt, crowded, prorsiradiate, flexuous, all with small outer ventrolateral clavi. Venter broad, flat, with strong siphonal keel and weak siphonal clavi equal in number to ventrolateral clavi but displaced adaperturally on phragmocone. Ornament declines on adult body chamber, which may be constricted; umbilical bullae present, flank ribs decline but ventrolateral ornament persists; siphonal clavi become irregular.

The suture is very simple with broad bifid E/L with few incisions, narrower L, and nearly entire L/U_2.

DISCUSSION: Decline in ornament and the development of constrictions indicates that the species attains maturity at 17 mm or less, while the very simple adult suture indicates

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Fig. 65. *Prionocyclus macombi* Meek, 1876. **A, B**. USNM 498361; **C, D**. USNM 498362, both gracile forms. **E–G**. USNM 498363, robust form. **H–J**. USNM 498364; **K, L**. USNM 498365; **M, N**. USNM 498366; **O–Q**. USNM 498367, all gracile forms. **R–T**. USNM 498368, robust form; **U–W**. USNM 498369; **X, Y.** USNM 498370, both gracile forms; **Z, A¹.** USNM 498371, robust form. All specimens are from locality 6. All figures are ×1.

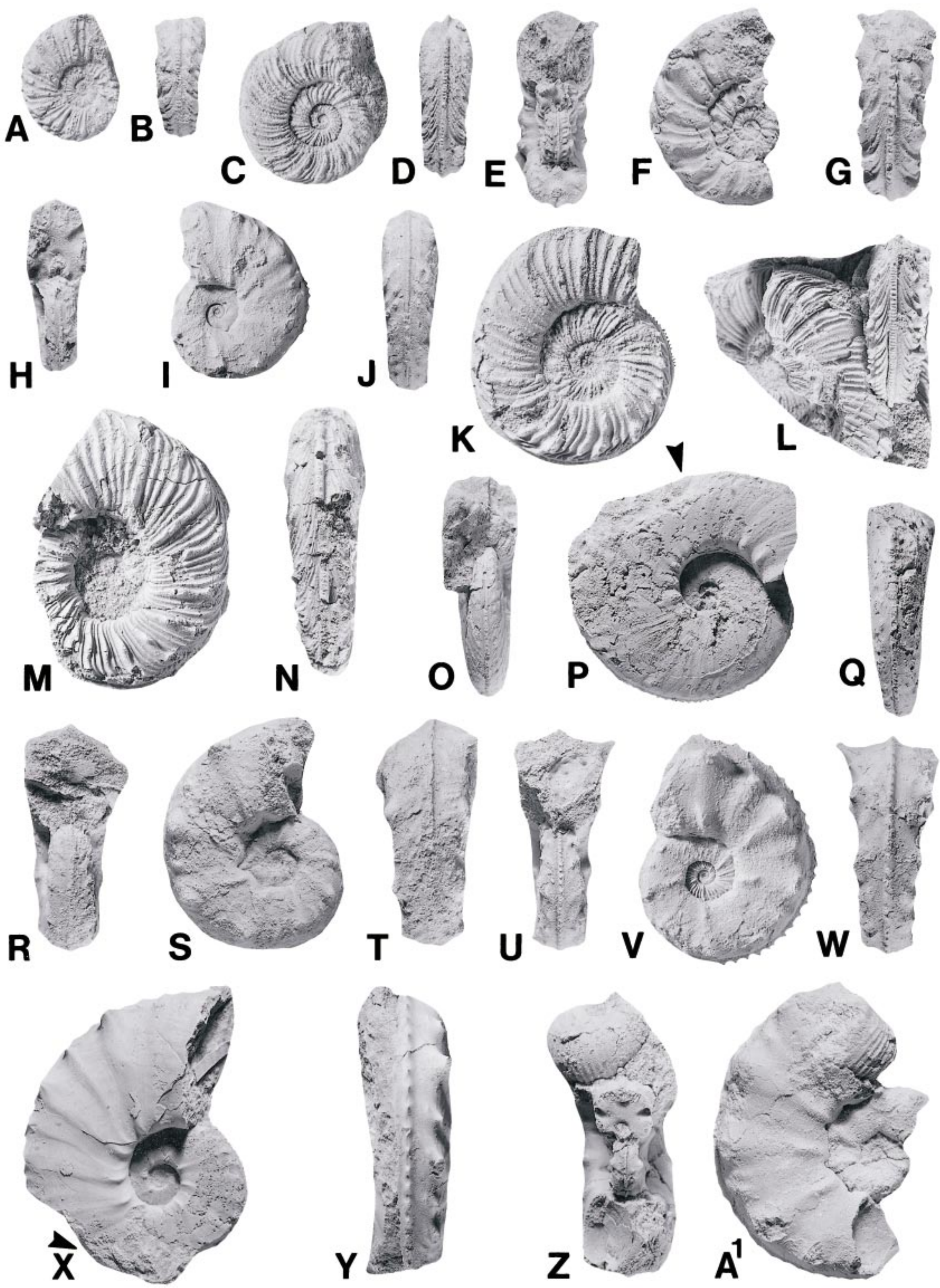
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Fig. 66. *Prionocyclus macombi* Meek, 1876. USNM 498372, a robust form from locality 6. All figures are ×1.

that these specimens are more than mere juveniles of some larger form. *Collignonicerites* resembles *Collignoniceras*; the very simple suture of *Collignoniceras* (e.g., Matsumoto, 1965: text-fig. 6A) is retained to maturity in *Collignonicerites*. The phragmocone ornament of *Collignonicerites* with outer ventrolateral clavi equal in number to siphonal clavi and ribs springing in groups from bullae resembles that of the ornamented earliest developmental stages of *Collignoniceras* with which *Collignonicerites collisniger* gen. et sp. nov. co-occurs.

Collignonicerites is an analog of *Prionocyclites* Kennedy, 1988, a diminitive genus closely related to *Prionocyclus*. Species of the two genera share certain features common to progenetic dwarfs, including a greatly simplified suture. However, they differ in that species of *Prionocyclites* are more evo-

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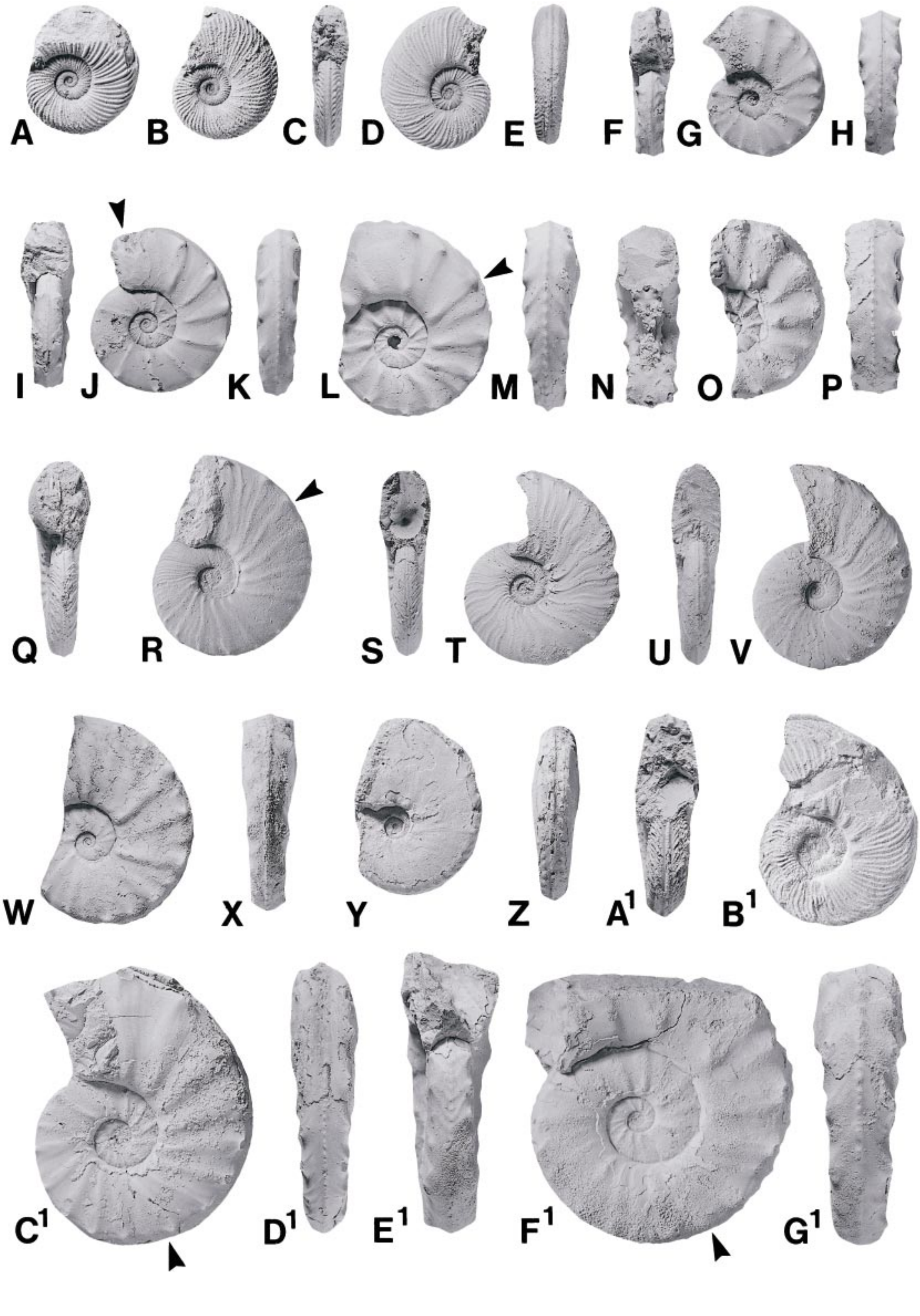
Fig. 67. *Prionocyclus macombi* Meek, 1876. **A**. USNM 420139; **B**. USNM 498373; **C–E**. USNM 498374, all gracile forms; **F–H**. USNM 498375; **I–K**. USNM 498376; **L, M**. USNM 498377; **N–P.** USNM 498378, all robust forms. **Q, R**. USNM 498379; **S, T**. USNM 420138; **U, V**. USNM 420136, all gracile forms. **W, X**. USNM 498380, robust form. **Y, Z**. USNM 498381; **A¹, B¹.** USNM 498382, both gracile forms. **C¹, D¹.** USNM 498383; **E¹–G¹.** USNM 498384, both robust forms. A–X, C¹–G¹ are from locality 36; Y-B¹ are from locality 38. Figures A–E are ×2; figures F–G¹ are ×1.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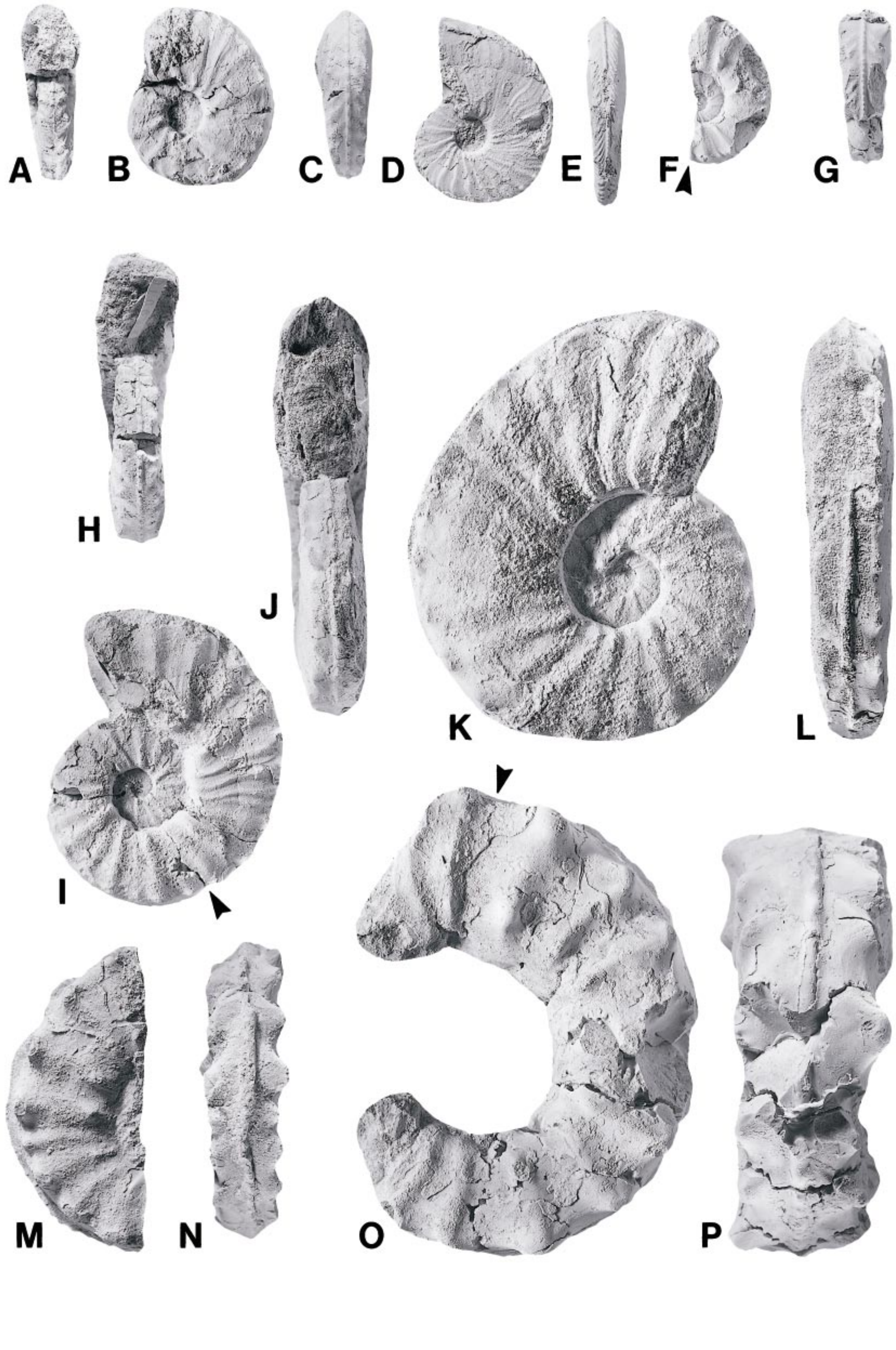
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lute and lack massive bullae giving rise to groups of ribs, having instead narrow, distant, single bullate primaries separated by nonbullate primaries and secondaries, an undulose rather than serrated keel, and a body chamber with distant feeble bullae, narrow, single flank ribs, and an apertural constriction flanked by collar-ribs.

Progenetic species have increasingly been described in recent publications on Late Cretaceous ammonites, as noted by Wright (1996: xviii; see, for instance, Wright and Kennedy, 1980; Kennedy, 1988; Kennedy and Cobban, 1990a, 1990b). Dimorphism has been recognized in these dwarfs, demonstrating that they are not the microconchs of co-occurring larger taxa. Because of their small size, these dwarf taxa have, in general, only been detected in exceptionally preserved faunas, such as those found in the concretions in shale and mudstone facies of the U.S. Western Interior.

OCCURRENCE: Middle Turonian *Collignoniceras woollgari regulare* Subzone of the Black Hills only.

Collignonicerites collisniger, new species
Figure 49A–K, M–T

DERIVATION OF NAME: *collis* + *niger* (Latin) black hills, from the type area.

TYPES: Holotype is USNM 498294 (fig. 49M, R–T), paratypes USNM 498295–498302 (fig. 49A–K, N–Q; 498301 not illustrated), from the middle Turonian Carlile Shale, *Collignoniceras woollgari regulare* Subzone at locality 12 in fig. 1: USGS Mesozoic locality D13832, Carlile Shale, middle Turonian, *C. woollgari regulare* Subzone, sec. 35, T. 8 S, R. 1 E, Fall River County, South Dakota.

DIAGNOSIS: With the characters of the genus.

DESCRIPTION: Coiling fairly involute (U/D = 0.26) and umbilicus moderately deep (table 6). The umbilical wall is flattened, subvertical, with an evenly rounded shoulder. The whorl section is compressed, with greatest breadth below midflank in intercostal section, and shows broadly rounded inner flanks, flattened convergent outer flanks, and a relatively broad, flattened venter with a sharp siphonal keel. The greatest breadth is at the umbilical bullae in costal section. In strongly ornamented variants, blunt umbilical bullae, four to six per whorl, are present in middle growth. The bullae give rise to two or three primary ribs with up to three nonbullate long ribs separating the bullate groups. These nonbullate ribs arise either singly or in pairs at the umbilical shoulder to give a total of 16 ribs per half whorl. Ribs are broad, crowded, flexuous, and prorsiradiate, and each bears a small outer ventrolateral clavus from which the rib projects forward and declines in strength, intersecting the line of the siphonal keel in an acute chevron. The keel has even siphonal clavi, equal in number to but displaced adaperturally of the ventrolateral clavi. In feebly ornamented variants, the umbilical bullae are weak; the flanks bear only striae and lirae on the inner part but the ventrolateral part is similar to that already described. The umbilical bullae may decline on the adult body chamber, which may be constricted, while the crenulations on the siphonal keel become irregular.

The suture is the same as for the genus.

DISCUSSION: See under genus.

OCCURRENCE: As for types.

Genus *Prionocyclus* Meek, 1876
(= *Germariceras* Breistroffer, 1947)

TYPE SPECIES: *Prionocyclus serratocarinatus* Meek, 1871: 298, *non* Stoliczka, 1865: pl. 32, fig. 31, = *Prionocyclus wyomingensis* Meek, 1876a: 452.

DIAGNOSIS: Medium to large, adult up to 300 mm in diameter. Size-related dimorphism not recognized (due to paucity of adults), but the middle growth stages of all

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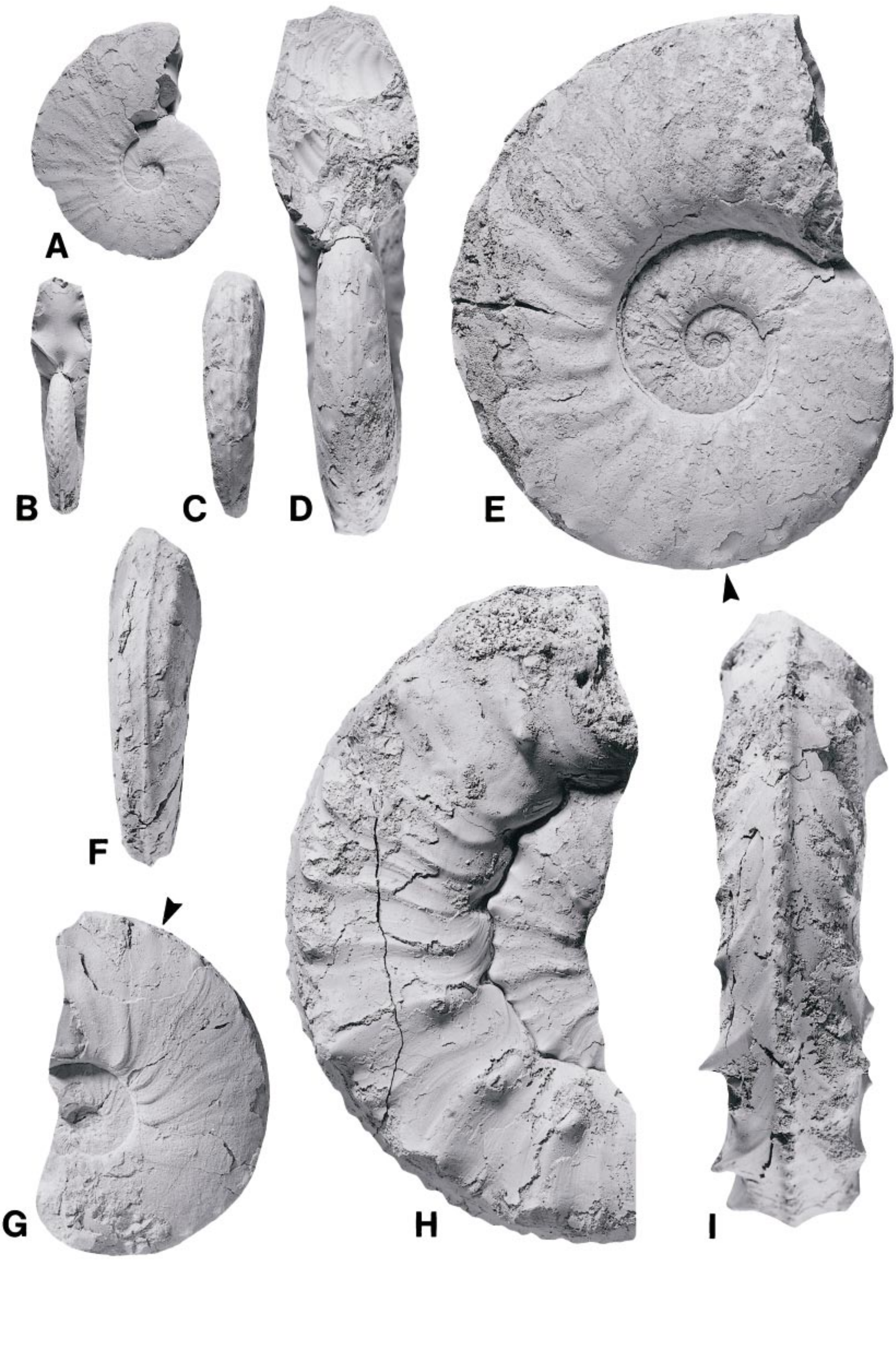
Fig. 68. *Prionocyclus macombi* Meek, 1876. **A–C**. USNM 498385, gracile form from locality 56. **D, E**. USNM 498386, gracile form from locality 55. **F, G**. USNM 498387, robust form from locality 56. **H, I.** USNM 498388, robust form from locality 55. **J–L**. USNM 498389, gracile form from locality 55. **M, N**. USNM 498390; **O, P**. USNM 498391, both robust forms from locality 56. All figures are ×1.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species occur as involute, relatively compressed, feebly ornamented gracile forms or more evolute, less compressed, strongly ornamented, robust forms. Ornament highly variable, typically of stronger primary ribs with umbilical, inner, and outer ventrolateral tubercles at some stage in ontogeny separated by weaker nonbullate and intercalated ribs that have inner and outer ventrolateral tubercles at some stage in ontogeny. Outer ventrolateral tubercles may decline or not, inner ventrolateral tubercles may bear long septate spines; faint inner lateral tubercles may develop during later growth stages. Siphonal keel is strong to weak, and finely serrated, with the number of serrations exceeding the number of ribs.

DISCUSSION: The type species of *Prionocyclus* and *Collignoniceras* are distinct, especially in the adult stage, and juveniles can be separated because the keel of *Collignoniceras* has siphonal clavi equal in number to that of the ventrolateral tubercles, whereas in *Prionocyclus* the serrations greatly outnumber the ribs (compare figs. 17, 18 and figs. 78, 84). In *Prionocyclus*, the marked differentiation of ribbing present in the early ontogenetic stages of certain variants of *C. praecox* (e.g., fig. 41F–U) persists to maturity.

Germariceras Breistroffer, 1947 (unpaged), with *Ammonites germari* Reuss, 1845 (fig. 109K), from the upper Turonian of Czech Republic as type species, is best known from the lithographs of Fritsch (1872: pl. 14, figs. 1, 2; pl. 16, fig. 7), and was recently revised by Kaplan (1988). It is here shown to be common and widespread in the U.S. Western Interior, and shows no characters that merit separation from *Prionocyclus*.

OCCURRENCE: Middle Turonian of the U.S. Western Interior, Gulf Coast, and northern Mexico; upper Turonian of the U.S. Western Interior, Gulf Coast, and northern Mexico, Tunisia, Japan, Czech Republic, Germany, and Kazakhstan. Records from Southeast France (Middlemiss and Moullade, 1968) are unsubstantiated.

Prionocyclus hyatti (Stanton, 1894)

Figures 50–60

Prionotropis hyatti Stanton, 1894: 176, pl. 42, figs. 5–8.

Prionocyclus hyatti Stanton. Logan, 1898: 468, pl. 102, figs. 5–8.

Prionocyclus hyatti Stanton. Grabau and Shimer, 1910: 228, fig. 1509e–g.

Prionocyclus hyatti Stanton. Diener, 1925: 156.

Prionotropis aff. *woollgari* (Mantell). Moreman, 1927: 97 (*pars*), pl. 13, fig. 2.

Prionotropis aff. *P. hyatti* Stanton. Adkins, 1928: 250.

Prionotropis eaglensis Adkins, 1928: 250, pl. 32, figs. 1, 2.

Pseudaspidoceras eaglense (Adkins). Adkins, 1931: 53.

Prionotropis graysonensis (Shumard). Moreman, 1942: 213.

Prionocyclus aff. *woollgari* Meek (not Mantell). Moreman, 1942: 214.

Prionotropis woollgari Meek (?*non* Mantell). Haas, 1946: fig. 45.

Collignoniceras hyatti (Stanton). Cobban, 1951: 2188, 2191, 2192, fig. 2.

Collignoniceras hyatti (Stanton). Cobban and Reeside, 1952: 1018.

Collignoniceras hyatti (Stanton). Cobban, 1955: 204, pl. 2, fig. 10.

Collignoniceras hyatti (Stanton). Hattin, 1962: 79, pl. 24, figs. A–E.

Prionocyclus hyatti (Stanton). Powell, 1963: 1220, pl. 166, figs. 1, 8–12; text-fig. 5a, c, d, f–h.

Collignoniceras hyatti (Stanton). Hattin, 1965: fig. 4 (4).

Prionocyclus hyatti (Stanton). Matsumoto, 1965: 19, pl. 17, fig. 3.

Prionocyclus hyatti (Stanton). Cobban, 1976: 122, pl. 1, fig. 1.

Prionocyclus hyatti (Stanton). Kennedy and Cobban, 1976: pl. 8, fig. 3.

Prionocyclus hyatti (Stanton). Kauffman, 1977: pl. 22, fig. 1; pl. 26, fig. 7.

Prionocyclus hyatti (Stanton). Hattin, 1977: figs. 8 (9, 11).

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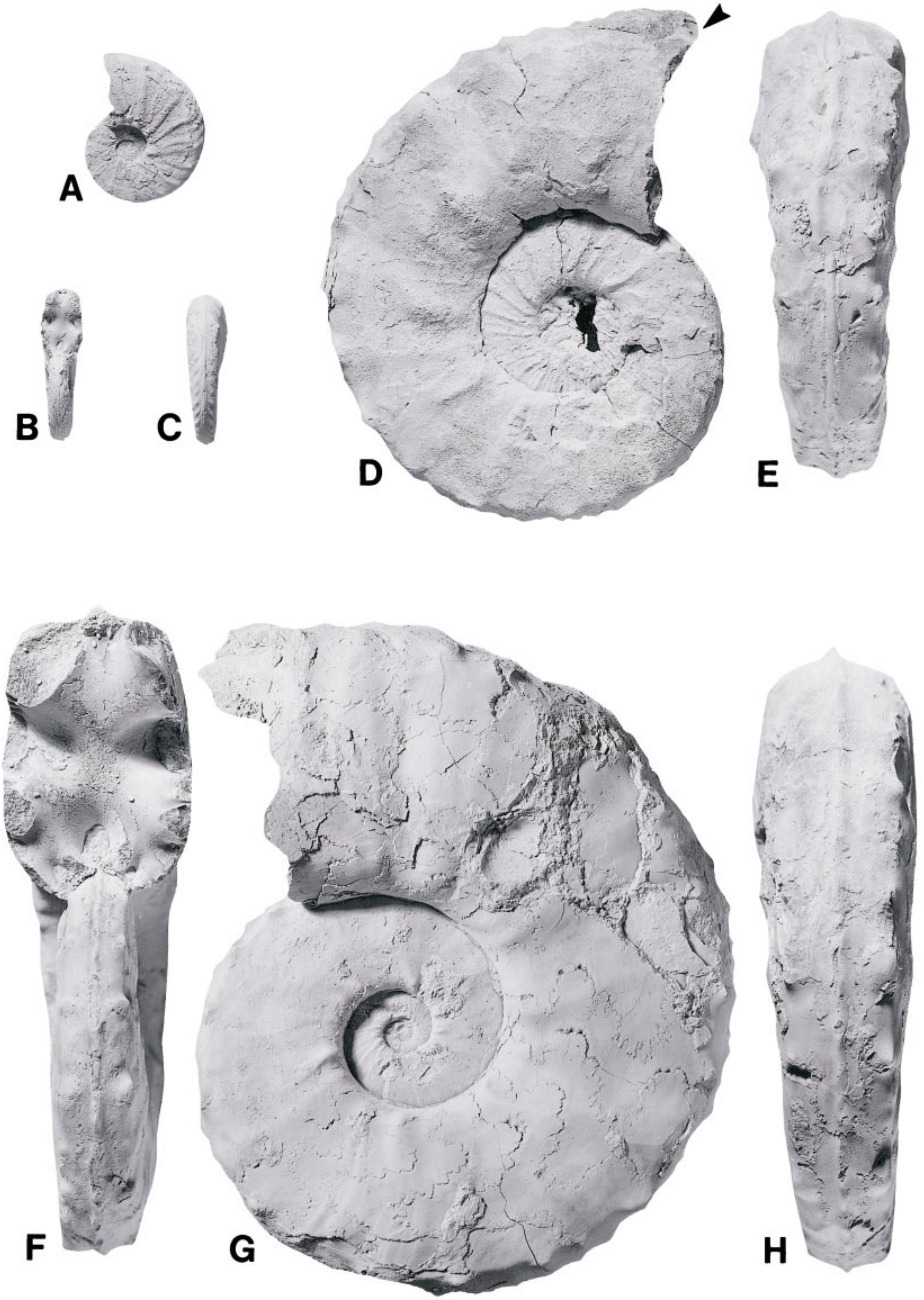
Fig. 69. *Prionocyclus macombi* Meek, 1876. **A–C**. USNM 498346, gracile form from locality 39. **D, E**. USNM 498392, gracile form from locality 36. **F, G**. USNM 498347, gracile form from locality 39. **H, I.** USNM 498393, robust form from locality 36. All figures are ×1.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Prionocyclus hyatti (Stanton). Hattin and Siemers, 1978: fig. 10.
Prionocyclus hyatti (Stanton). Kauffman et al., 1978: pl. 5, fig. 1.
Prionocyclus hyatti (Stanton). Young and Powell, 1978: pl. 1, figs. 1–3, 7, 8.
Prionocyclus hyatti (Stanton). Merewether et al., 1979: pl. 3, figs. 1, 2.
Prionocyclus hyatti (Stanton). Cobban, 1984a: 85.
Prionocyclus hyatti (Stanton). Cobban, 1986: fig. 3Q.
Prionocyclus hyatti (Stanton). Kennedy, 1988: 75, pl. 15, figs. 1–24; pl. 16, figs. 1–20; pl. 17, figs. 1–7; text figs. 24d, e, f, 25–27, 31b.
Prionocyclus hyatti (Stanton, 1894). Kennedy and Cobban, 1988: 606, figs. 7. 1–8, 11.
Prionocyclus hyatti (Stanton, 1894). Kennedy et al., 1989: 89, figs. 24f, g, m, 25, 26a, b, 27a–j, s–w.
Prionocyclus hyatti (Stanton). Cobban and Hook, 1989: fig. 9i, j.
Prionocyclus hyatti (Stanton). Cobban, 1990: pl. 5, figs. 3–5.
Prionocyclus hyatti (Stanton, 1894). Emerson et al., 1994: 210, unnumbered figures on pp. 210, 211.
Prionocyclus hyatti Stanton, 1893. Kirkland, 1996: 99, pl. 50, figs. L, M.
Prionocyclus hyatti (Stanton, 1894). Reyment and Kennedy, 2001; fig. 2a–d.

TYPES: Lectotype, by subsequent designation of Matsumoto 1965: 19, is USNM 22941, the original of Stanton's 1894: plate 42, figures 5, 6 (fig. 50C–E); figured paralectotype is USNM 22941a, the original of Stanton's plate 42, figures 7, 8 (fig. 50A, B). They are from the Codell Sandstone (Pugnellus Sandstone) of Williams Creek and Poison Canyon, Huerfano Park, Colorado. Stanton refers to many specimens from Huerfano Park and a few from Coalville, Utah: all are paralectotypes (e.g., fig. 50F–H).

DIAGNOSIS: A moderately evolute fairly large species ornamented by straight, prorsiradiate primary and secondary ribs terminating in ventrolateral tubercles. Low keel differentiated into low asymmetric clavi slightly more numerous than the ribs. Inner whorls usually densely ribbed. Primary ribs on outer whorl support umbilical bullae or nodate umbilical tubercles. Inner ventrolateral tubercles on adult body chamber may enlarge into conspicuous spines.

DESCRIPTION: The lectotype is a small, robust specimen (Stanton, 1894: pl. 42, figs. 5, 6; Matsumoto, 1965: 19, pl. 17, fig. 3a–c; fig. 50C–E). Measurements in millimeters and ratios from a plaster cast are as follows: D = 31.0, Wb = 14.2 (46%), Wh = 12.0 (39%), Wb:Wh = 1.18, U = 10.6 (34%). Primary and secondary ribs arise on the umbilical wall and are straight and prorsiradiate on crossing the flanks. They number 29 per whorl at a diameter of approximately 7.5 mm, and 29 per whorl at a diameter of about 19 mm. Primary ribs support umbilical bullae, prominent clavate inner ventrolateral tubercles, and weak outer ventrolateral clavi. Some secondaries bear weaker ventrolateral tubercles. All ribs bend forward on the ventrolateral shoulder and fade out at an angle toward the keel. Most primaries and secondaries alternate. Toward the adapertural end, the inner ventrolateral tubercles on the primary ribs enlarge and become hornlike, projecting outward at a low angle to the venter. In this manner, the specimen is much like the last part of the phragmocone of the remarkable spined individual figured by Kennedy and Cobban (1976, pl. 8, fig. 1; fig. 58) from the Carlile Shale of Kansas. On the older part of the outer whorl of Stanton's specimen, the keel is differentiated into low clavi that correspond to the ribs, but on the younger part, the clavi seem to number about two per rib.

The other specimen figured by Stanton (1894: pl. 42, fig. 7; fig. 50A, B) is a small, gracile, evolute specimen 21.0 mm in diameter with an umbilical ratio of 49% (measurements from a plaster cast). The keel is low and appears to be differentiated into asymmetric clavi that are less numerous than the ribs. Ribs are narrow and prorsiradiate; they number 35 on the outer whorl, where one or two secondaries separate primaries.

In the lower, *Hoplitoides sandovalensis*

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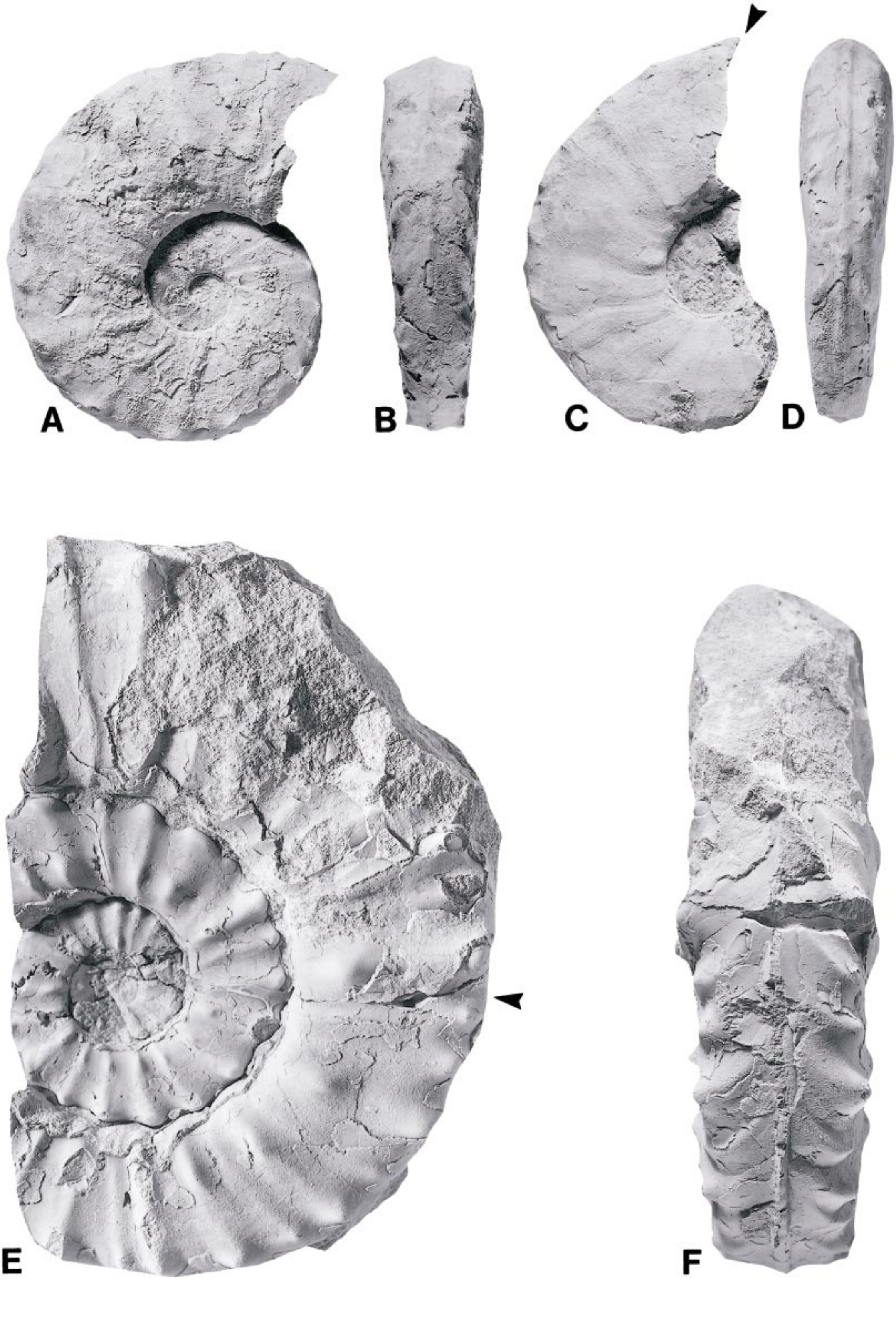
Fig. 70. *Prionocyclus macombi* Meek, 1876. **A–C**. USNM 498344; **D, E**. USNM 498394; **F–H**, USNM 498349, all gracile forms from locality 39. All figures are ×1.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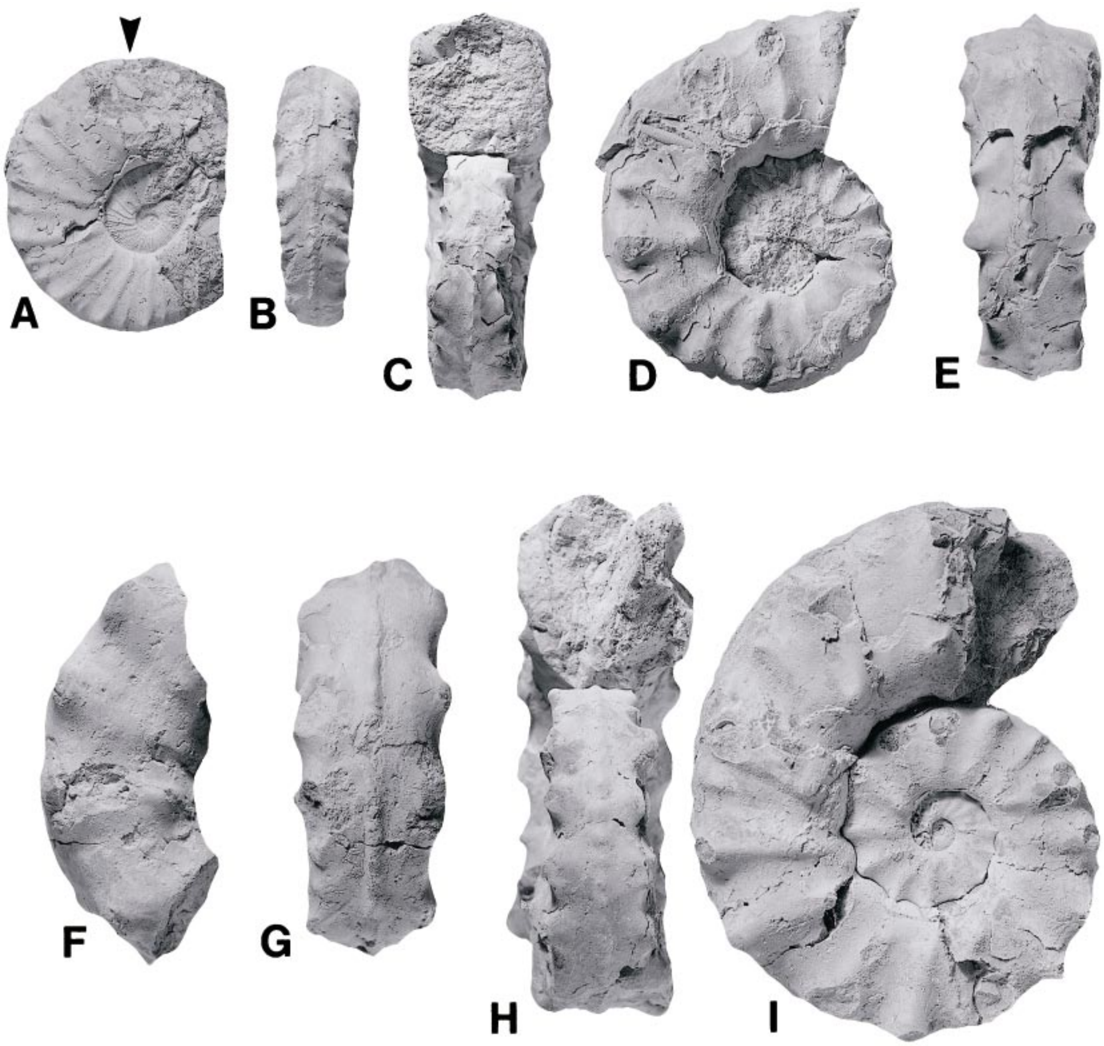

Fig. 72. *Prionocyclus macombi* Meek, 1876. **A, B**. USNM 498397; **C–E**. USNM 498340; **F, G**. USNM 498398; **H, I**. USNM 498341, all robust forms from USGS Mesozoic locality 39. All figures are ×1.

Subzone of the *Prionocyclus hyatti* Zone, a collection from a narrow horizon in the Semilla Sandstone Member of the Mancos Shale at USGS locality 28873 (locality 41 in fig. 1) is typical. It and other collections reveal that both robust and gracile forms are present in similar numbers.

In the robust form (figs. 55C, D, 56–58), nuclei show great variation. Coiling is very evolute, with the umbilical seam indented to accommodate the inner ventrolateral tubercles of the inner whorl, the umbilicus is of moderate depth, the umbilical wall flattened and subvertical, the umbilical shoulder quite

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Fig. 71. *Prionocyclus macombi* Meek, 1876. **A, B**. USNM 498348; **C, D**. USNM 498395, both gracile forms from locality 39. **E, F**. USNM 498396, robust form from locality 55. All figures are ×1.


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narrowly rounded, the whorls slightly compressed to depressed, quadrate in intercostal section, and octagonal in costal section (table 7). At one extreme there are as few as 20 ribs per whorl, with up to 30 at the other. The ribs are all bullate primaries of equal development, strong, straight, and prorsiradiate, and strengthen across the flanks to strong conical to clavate inner ventrolateral tubercles. A broad prorsiradiate rib connects an inner ventrolateral tubercle to a strong outer ventrolateral clavus, and a smooth zone separates the ribs from a strong siphonal keel, with clavi occupying the interspaces between tubercles (fig. 56C–D). As size increases, the ribs become very coarse and massive, with strong (fig. 56H–J) to weak bullae (fig. 56C, D), with as few as 16 ribs per whorl. Sometimes the bullae are of variable strength (fig. 56E–G), and displaced out from the umbilical shoulder. The outer ventrolateral clavi are assimilated into the inner ventrolateral tubercles, which enlarge into massive blunt horns that project outward but usually not significantly above the level of the venter (fig. 56E–J). Other robust individuals have nuclei in which strong, bullate primary ribs are separated by up to three weaker nonbullate primaries, with a total of up to 45 ribs per whorl. This differentiation persists into middle growth. The bullate primaries have strong umbilical bullae and inner and outer ventrolateral tubercles. The nonbullate primaries sometimes connect to the umbilical bullae as mere striae and have weak ventrolateral tubercles, in some cases, only outer ones. In some specimens (fig. 58) the stronger primaries develop massive horns or spines, with hornless ribs between. The largest robust individual at hand is 270 mm in diameter.

Nuclei of the gracile form (figs. 51A–R, V–Y, 52A–L, 53, 54, 55E–J) overlap to a degree with those of the robust form. They are more compressed, with a broad, shallow umbilicus (table 7), and have up to 50 ribs per whorl that may be even (fig. 51M–O) or vary greatly in strength (fig. 51A–I). The stronger

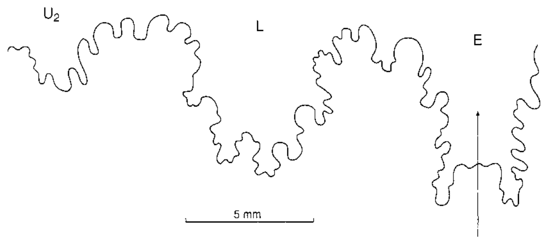

Fig. 74. External suture of *Prionocyclus macombi* Meek, 1876, from USNM 498854, from locality 36.

ribs are flared, usually bullate, with inner and outer ventrolateral tubercles; the weaker ribs lack bullae and have feeble or no inner ventrolateral tubercles. This style of ornament may persist into middle growth, and there are gracile forms with dense, even ribs that may reduce to mere striae (fig. 51N) and others with ribbing of variable strength and tubercle development (fig. 52K, L). Inner and outer ventrolateral tubercles remain separate and do not merge into horns, as in the robust form; nonbullate ribs may lack an inner ventrolateral tubercle and have much weaker outer ventrolateral tubercles than on the bullate primaries. The keel is broadly and irregularly undulose.

Both robust and gracile forms show enormous variation in ribbing and tuberculation style as well as timing of ontogenetic changes in ornament. This is more readily appreciated from the illustrations (figs. 50–60) than from mere description.

Prionocyclus hyatti from the upper part of its zonal range is illustrated by collections from the Carlile Shale of Kansas, where the species occurs as fragments, often of large body chambers, in ironstone concretions. Original aragonite shell is often preserved (fig. 57). Many of the specimens we have seen from Kansas are large, up to 300 mm in diameter. Juveniles are as variable as those from the *Hoplitoides sandovalensis* Subzone in New Mexico and elsewhere already described, with even, coarse to fine ribbing as well as markedly differentiated weak and

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Fig. 73. *Prionocyclus macombi* Meek, 1876. **A, B**. USNM 498399; **C, D**. USNM 498342, both robust forms from USGS Mesozoic locality 39. All figures are ×1.

TABLE 8
Dimensions of juvenile *Prionocyclus macombi* Meek, 1876[a]

Specimen	D	Wb	Wh	Wb:Wh	U	Ribs
USNM 498350	15.2 (100)	4.2 (0.28)	6.5 (0.43)	0.65	6.5 (0.43)	87
USNM 498351	20.4 (100)	4.8 (0.23)	9.0 (0.44)	0.53	6.0 (0.29)	98
USNM 498352	20.5 (100)	4.9 (0.24)	10.4 (0.51)	0.47	5.8 (0.28)	84

[a] See table 1 for explanation of symbols. Ribs = number of ribs per whorl. All measurements are on costal sections.

strong ribs. This variation is maintained into middle growth, and most individuals have strong, bullate primary ribs with massive ventrolateral horns and weaker, nonbullate intercalated ribs between that have weak ventrolateral tubercles. At the largest diameters, fragments may bear as few as six ribs with massive ventrolateral horns per half whorl, and some specimens show the horns to have been septate, with a long spine (fig. 59).

These large specimens commonly show an outward migration of the umbilical bullae, which become conical and occupy an inner flank position. The keel of these specimens is variable, from broadly undulose with coarse clavi only slightly more numerous than ventrolateral tubercles (fig. 57A, B) to others where the crenulations are minute and far more numerous.

The suture (fig. 60) has moderately incised elements; E/L is broad and bifid, and L is narrower and bifid, as is L/U_2.

DISCUSSION: *Prionocyclus hyatti* is the species of the genus closest to *Collignoniceras*, discussed above. Juvenile stages show certain common characters, but middle and late growth stages are distinct. *Prionocyclus hyatti* differs from the most closely comparable *Prionocyclus*, *P. macombi*, as follows: the robust forms of the two species may have a degree of overlap in their coiling, whorl section, and expansion rate, but small and medium-sized individuals of *P. macombi* never develop ventrolateral horns as massive as those of *P. hyatti*, nor the striking differentiation into strong horned ribs with umbilical bullae, and weak, nonbullate hornless ribs. The gracile forms of *P. macombi* are much more compressed, higher-whorled, and more involute than the corresponding forms of *P. hyatti*. The

TABLE 9
Dimensions of *Prionocyclus macombi* Meek, 1876[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
Robust forms						
USNM 498340	Costal	53.0 (100)	20.0 (37.7)	17.9 (33.8)	1.12	13.0 (24.5)
	Intercostal	49.5 (100)	16.5 (33.3)	16.4 (33.1)	1.01	13.0 (26.3)
USNM 498341	Costal	64.5 (100)	23.0 (35.8)	22.5 (36.9)	1.02	27.0 (42.0)
	Intercostal	61.0 (100)	19.5 (32.0)	22.3 (36.6)	0.87	27.0 (44.3)
USNM 498342	Costal	96.5 (100)	34.5 (35.8)	35.0 (36.3)	0.99	38.2 (39.6)
	Intercostal	96.5 (100)	28.5 (29.5)	35.0 (36.3)	0.81	38.2 (39.6)
USNM 498343	Costal	122.0 (100)	40.3 (33.0)	41.7 (34.1)	0.97	47.3 (38.8)
	Intercostal	121.0 (100)	36.8 (30.4)	41.7 (34.5)	0.88	47.3 (39.0)
Gracile forms						
USNM 498344	Costal	21.4 (100)	5.8 (27.1)	10.7 (50.0)	0.54	5.0 (23.4)
USNM 498345	Costal	32.0 (100)	8.2 (25.6)	16.5 (51.5)	0.50	5.2 (16.3)
USNM 498346	Costal	39.4 (100)	9.9 (25.1)	18.5 (47.0)	0.54	8.7 (22.1)
USNM 498347	Costal	60.0 (100)	15.5 (25.8)	26.0 (43.3)	0.60	13.7 (22.8)
USNM 498348	Costal	67.2 (100)	18.0 (26.8)	29.0 (43.2)	0.62	16.1 (24.0)
USNM 498349	Costal	114.5 (100)	31.5 (27.5)	47.5 (41.5)	0.66	37.0 (32.3)

[a] See table 1 for explanation of symbols.

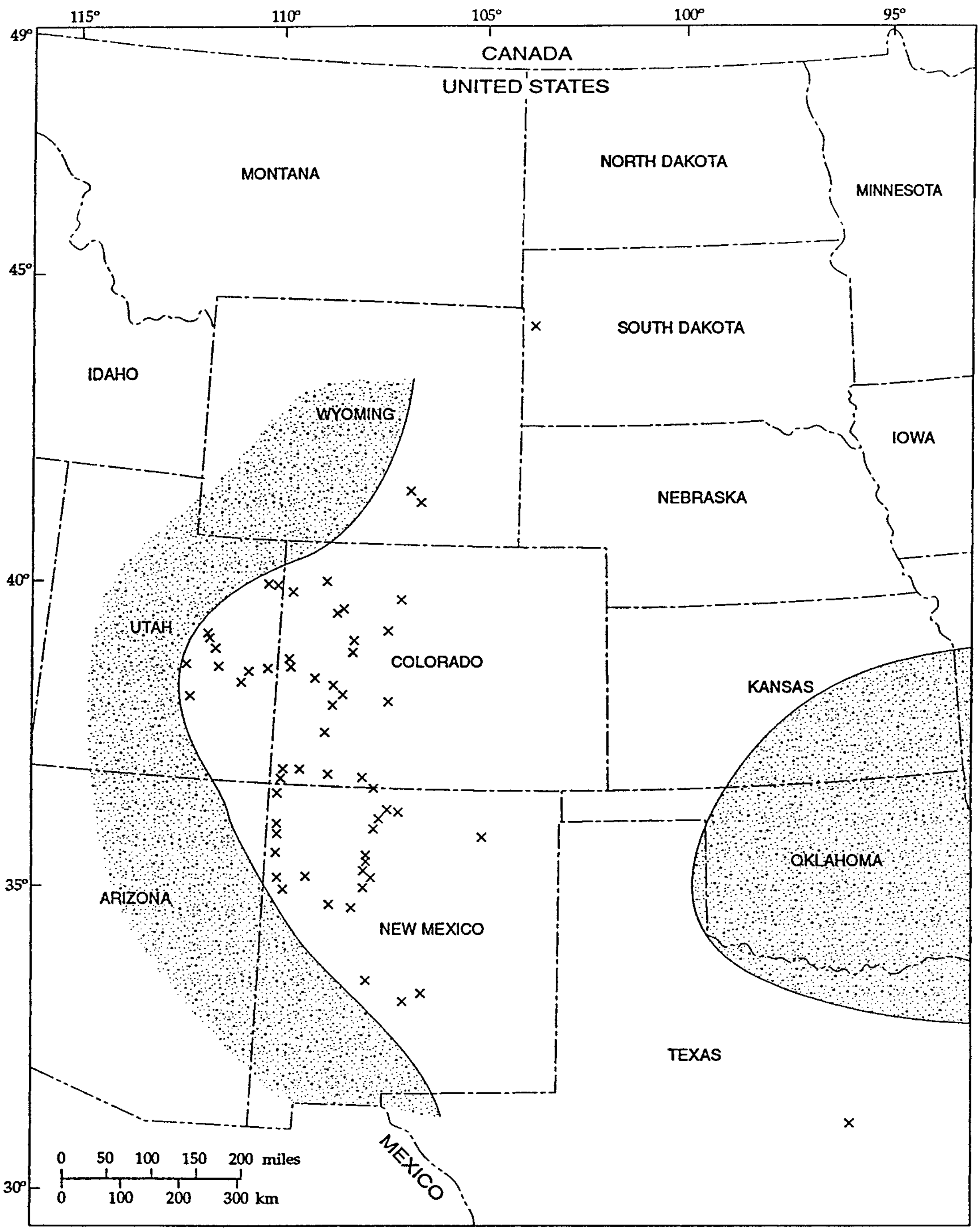

Fig. 75. Distribution of *Prionocyclus macombi* Meek, 1876, in the Western Interior Seaway during the middle Turonian. Land areas indicated by stipple.

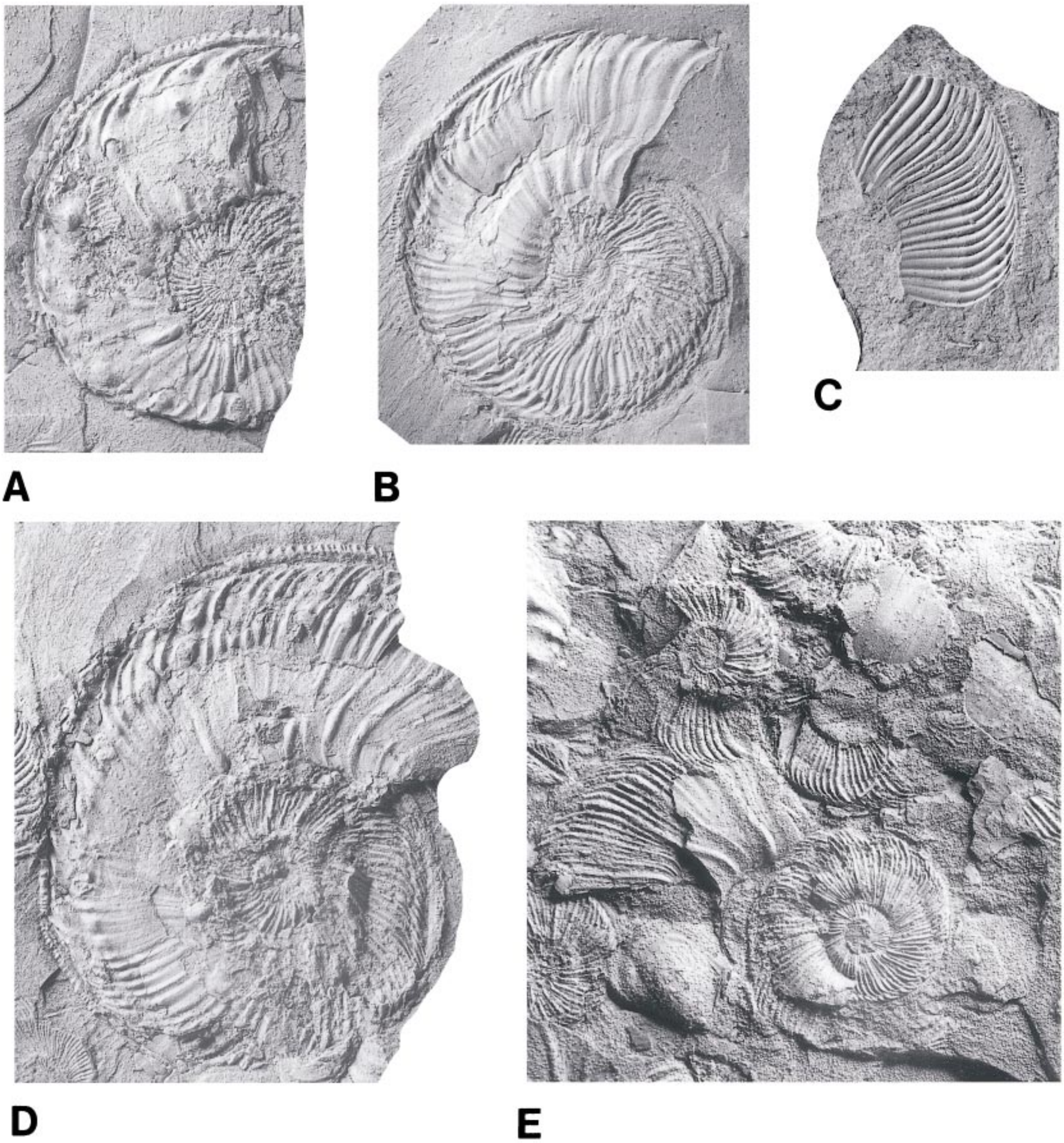

Fig. 76. *Prionocyclus bosquensis* Kennedy, 1988. **A**. Paratype OUM KT 3858. **B**. Paratype OUM KT 3281. **C.** Paratype OUM KT 3801b. **D**. Holotype, OUM KT 3854. **E**. Paratype OUM KT 3869. All specimens are from the upper Turonian *Scaphites whitfieldi* Zone, South Bosque Formation, 10 km (6 mi) southwest of Waco, McLennan County, Texas. All figures are ×2.

ribbing is also denser and finer in *P. macombi* with the ribs often reduced to mere striae, and the inner and outer ventrolateral tubercles of the inner whorls replaced by a single ventrolateral clavus at an early stage.

OCCURRENCE: Widely distributed in the Western Interior from northern Montana southward into Trans-Pecos Texas and eastward from there into central and northern Texas (fig. 61). Also known from northern Chihuahua, Mexico, and Kazakhstan (Marcinowski et al., 1996).

Fig. 77. *Prionocyclus bosquensis* Kennedy, 1988. **A**. Paratype OUM KT 3870. **B**. Paratype OUM KT 3868. **C**. Paratype OUM KT 3873. All specimens are from the lower upper Turonian *Scaphites whitfieldi* Zone, South Bosque Formation, 10 km (6 mi) southwest of Waco, McLennan County, Texas. All figures are ×1.

Prionocyclus albinus (Fritsch, 1872)

Figures 62, 108C

Ammonites albinus Fritsch, 1872: 28, pl. 6, fig. 4.
Ammonites albinus Fritsch. Diener, 1925: 23.
Prionocyclus hyatti (Stanton, 1894). Kennedy, 1988: 75 (*pars*), pl. 15, figs. 3–5; text-fig. 25H–L only.

TYPE: Lectotype, here designated, is the original of Fritsch, 1872: plate 6, figure 4, no. 03144 in the Collections of the Narodni Museum, Prague, from the Turonian of Wehlovice, in the Czech Republic (fig. 108C is a plaster cast taken from an external mold of the type).

DIAGNOSIS: A moderate-sized, fairly evolute species that has whorls higher than wide with flattened flanks. Ornament of numerous prorsiradiate ribs with primaries usually separated by two or three secondaries.

DESCRIPTION: The lectotype is 41 mm in diameter. Coiling is evolute, with U/D = 0.42. The umbilicus is shallow, with a feebly convex wall, and more narrowly rounded umbilical shoulder. On the last half whorl, six or seven primary ribs arise on the umbilical wall, and strengthen into feeble bullae perched on the umbilical shoulder. The ribs are coarse, straight, and prorsiradiate on the flanks, with inner and outer ventrolateral clavi; the venter is not preserved. These strong primaries are separated by single much weaker ribs that lack umbilical bullae and in-

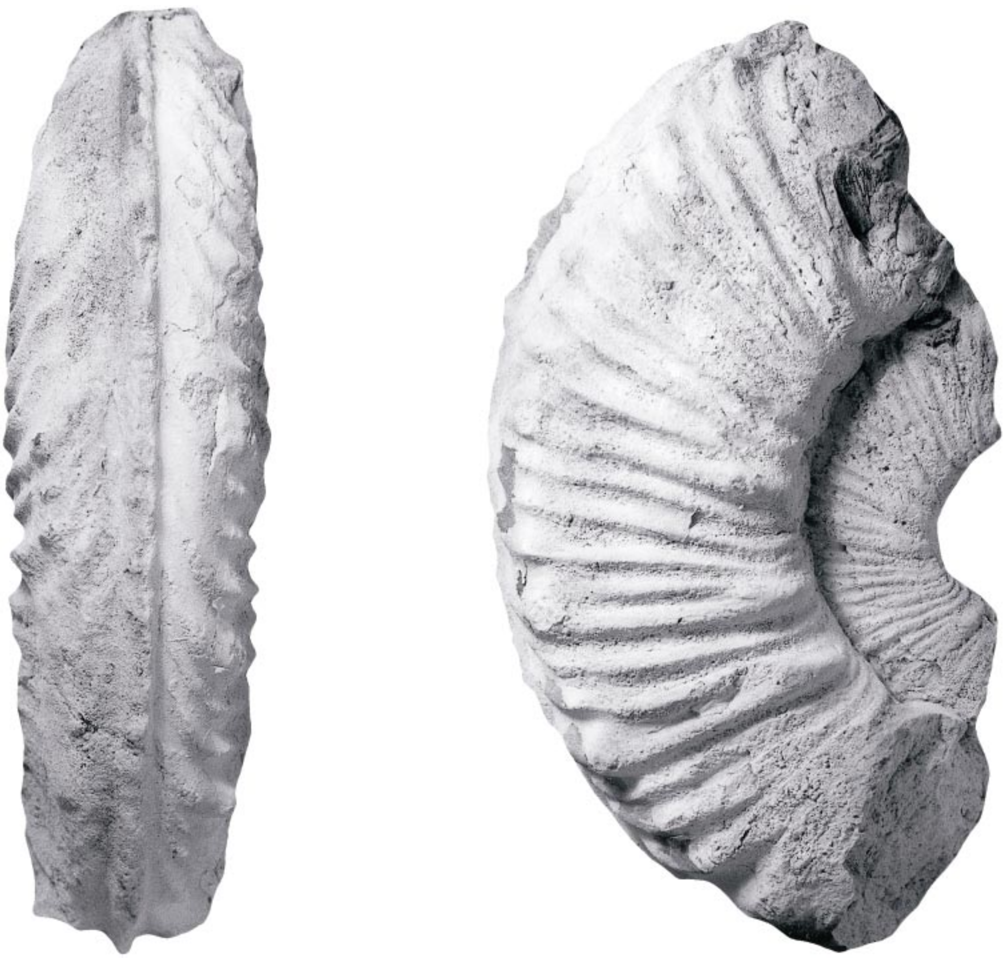

Fig. 78. *Prionocyclus wyomingensis* Meek, 1876. Lectotype, USNM 7729, middle Turonian *Scaphites warreni* Zone, Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. Figures are ×1.

ner ventrolateral tubercles. The poorly preserved inner whorls are much more finely ribbed.

Western Interior specimens referred to the species have finely and evenly ribbed inner whorls (fig. 62A, D, F, L, O); the ribs are equal, crowded, straight, and prorsiradiate on the flanks. This stage is succeeded, at variable diameters, by a growth stage in which the ribs differentiate into stronger primaries with umbilical bullae, strong inner, and weaker outer ventrolateral tubercles, separated by much weaker ribs that lack bullae and inner ventrolateral tubercles, but have feeble or effaced outer ventrolaterals; as many as four and as few as one of these weaker ribs may separate the stronger primaries. Ribbing of this type extends onto the body chamber of USNM 498339 (fig. 62P), interpreted as an adult.

The suture is moderately incised, as in *P. hyatti*.

DISCUSSION: *Prionocyclus albinus* may represent a paedomorphic derivative of *Prionocyclus hyatti* in which the crowded ornament and variable rib strength of juveniles of the latter are retained to maturity. Small specimens of the two species are liable to be confused, but in middle growth, the change to more distant ribbing in *P. hyatti* is dis-

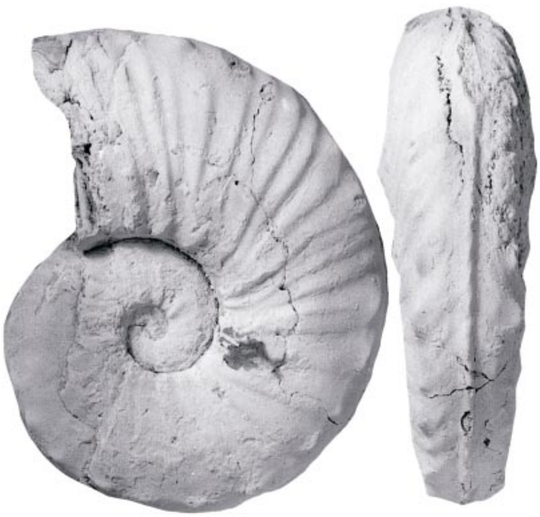

Fig. 79. *Prionocyclus wyomingensis* Meek, 1876. Paralectotype, USNM 7729, middle Turonian *Scaphites warreni* Zone, Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. Figures are ×1.

tinctive, and the two species reach maturity at widely differing diameters.

OCCURRENCE: *Prionocyclus hyatti* Zone, Smith County, Kansas; Emery County, Utah; Sandoval County, New Mexico; Dallas County, Texas. The type material is from the Turonian of the Czech Republic.

Prionocyclus macombi Meek, 1876

Figures 63–74

Prionocyclus? *macombi* Meek, 1876b: 132, pl. 2, fig. 3a–d.
Prionocyclus? *macombi* Meek. Stanton, 1894: 172, pl. 41, figs. 1–5.
Prionocyclus? *macombi* Meek. Logan, 1898: 264.
Prionocyclus macombi Meek. Johnson, 1903: 139.
Prionocyclus macombi Meek. Grabau and Shimer, 1910: 288, fig. 1510e–g.
Prionocyclus macombi Meek. Diener, 1925: 155.
Prionocyclus macombi Meek. Kauffman, 1977: pl. 26, figs. 4, 5.
Prionocyclus macombi Meek. Hook and Cobban, 1980: 46, text-fig. 5A–G.
Prionocyclus macombi Meek. Hill, 1982: fig. 22H, I.
Prionocyclus macombi Meek. Cobban, 1984a: 86.
Prionocyclus macombi Meek. Cobban, 1986: fig. 7D, E.
Prionocyclus macombi Meek, 1876b. Kennedy, 1988: 83, 84, pl. 2, fig. 11; pl. 18, figs. 4–9; text-figs. 28, 29b, e, j.
Prionocyclus macombi Meek. Emerson et al., 1994: 212, 378.
Prionocyclus macombi Meek, 1876. Reyment and Kennedy, 2001: figs. 2e–h, 4.

TYPES: The lectotype here designated is USNM 20259, the original of Meek, 1876b: plate 2, figure 3 (fig. 63A, B), from the Juana Lopez Member of the Carlile Shale of Colfax County, New Mexico, middle Turonian *Prionocyclus macombi* Zone. Meek refers to more than one specimen of *Prionocyclus*? *macombi* in his original account, indicating the species to be based on a type series. The lectotype is the original of his plate 2, figure 3a–c, and the original of his figure 3d may conceivably be the inner whorls of this specimen.

DIAGNOSIS: A moderate-size species that occurs as an early form with arched venter and a later form with flattened venter. Keel low and notched into as many as three or four clavi per rib. The gracile form is exceptionally compressed and has densely ribbed innermost whorls; the outer adult whorls are nearly smooth. The robust form has coarser and stronger ornament than the gracile form; ribs support nodate to bullate umbilical tubercles and nodate to spinose inner ventrolateral tubercles, whereas outer ventrolateral clavi are barely perceptible or absent.

DESCRIPTION: Robust and gracile forms of *Prionocyclus macombi* are distinct from the early growth stages on. During middle and later growth stages, it is also possible to recognize an early form of the species, where the venter is distinctively arched and rounded (figs. 68L, 71A–D, 72, 73) and a late form in which the venter is flattened (e.g., fig. 68P).

The earliest growth stages are highly variable and individuals may be nearly smooth (fig. 67Y, Z) to densely ribbed (fig. 67A–E) in the gracile form. The smoothest variants have distant umbilical bullae and tiny outer ventrolateral clavi, even though flank ornament is virtually absent. Densely ribbed juveniles generally have up to 16 strong primary ribs, sometimes feebly bullate, and giving rise to bundles of ribs. One to four weaker primary and intercalated ribs occur between the stronger ribs and extend to the

Fig. 80. *Prionocyclus wyomingensis* Meek, 1876. Paralectotype, USNM 7729, middle Turonian *Scaphites warreni* Zone, Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. Figures are ×1.

umbilicus or arise on the inner flank. Ribs are prorsiradiate and straight to feebly flexuous across the flanks. They project forward and are concave over the ventrolateral shoulder. Weak inner ventrolateral and clavate outer ventrolateral tubercles are present on the stronger primary ribs; the weaker primary and intercalated ribs are feebly or nontuberculate. This densely ribbed stage terminates abruptly in most specimens by about 15–20 mm diameter or less.

Dimensions, ratios, and number of ribs per whorl of three nuclei are given in table 8. At this stage, the shell is compressed and high-whorled with a small umbilicus comprising as little as 17% of the shell diameter with whorl breadth to height ratios of as little as 0.5. The umbilical wall inclines outward and merges with a broadly rounded umbilical shoulder. The flanks are flattened and subparallel, and the ventrolateral shoulders are broadly rounded. The venter is arched in early forms, and more flattened in later ones. Delicate umbilical bullae of variable strength

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Fig. 81. *Prionocyclus wyomingensis* Meek, 1876. **A, B**. USNM 498409; **C, D**. USNM 498410, both gracile forms from locality 29. All figures are ×1.

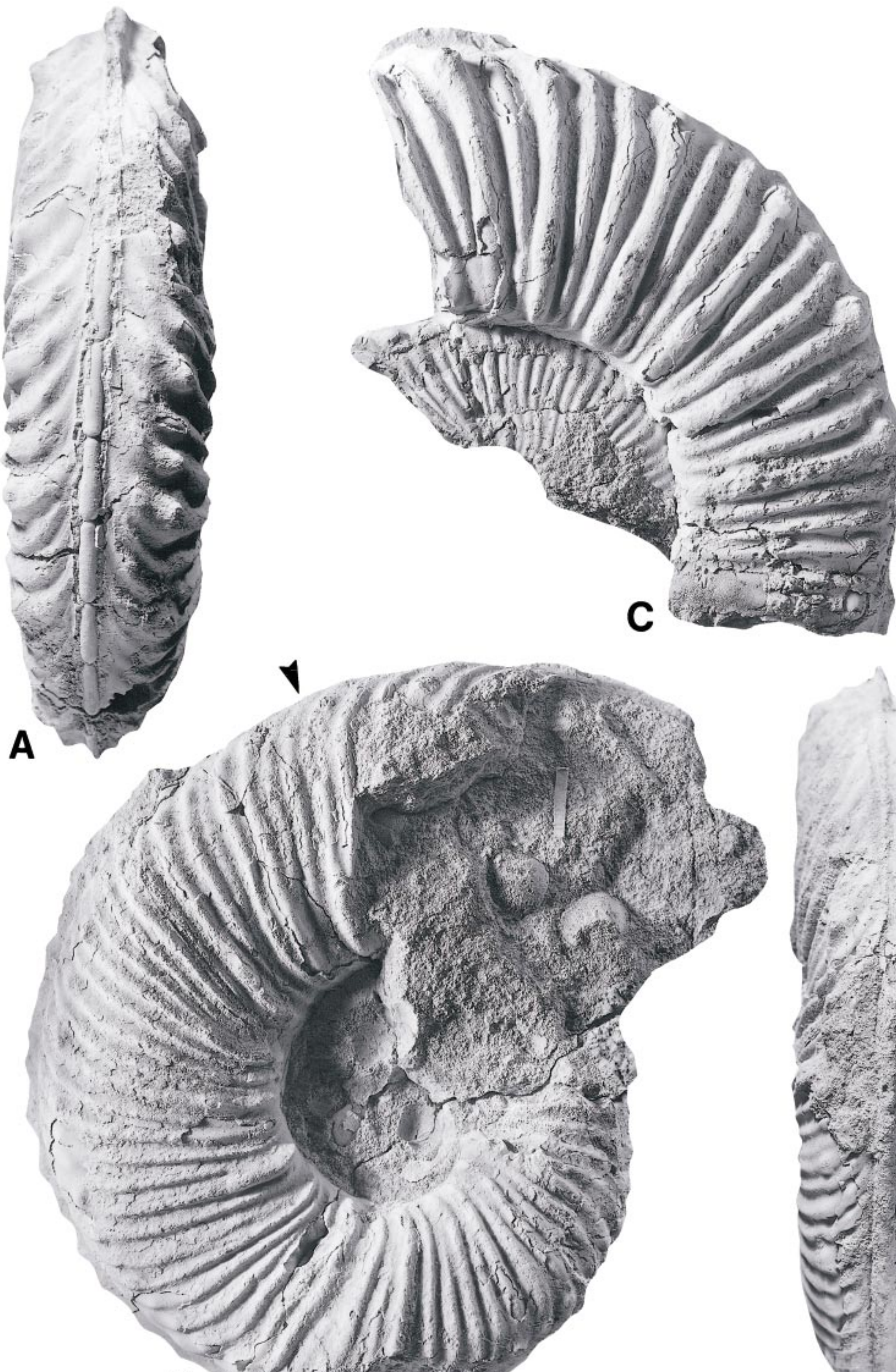


Fig. 82. *Prionocyclus wyomingensis* Meek, 1876. USNM 7729D. This specimen bears the label 7729 in the same hand as the figured syntypes, and appears to be a previously unrecognized syntype, now paralectotype of the species. Middle Turonian *Scaphites warreni* Zone, Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. Figure is ×0.9.

and generally 14–20 per whorl perch on the umbilical shoulder (fig. 67Q–X). They give rise to narrow, flexuous prorsiradiate ribs that terminate in small clavate to bullate inner ventrolateral tubercles. Outer ventrolateral tubercles may also be present, linked to the inner by prorsiradiate ribs, but disappear in early middle growth. The wide interspaces between these bullate primaries bear weak ribs that arise at the umbilical seam or low on the flanks plus lirae and growth striae (fig. 67Q–X). These weaker ribs may bear inner, but not outer ventrolateral tubercles, giving the shell a distinctive appearance when viewed ventrally (fig. 69B, C). Ornament sweeps forward and is concave over the ventrolateral shoulder, forming an acute ventral chevron. The keel is minutely and evenly serrated, the serrations far exceeding the ribs in number (figs. 69A–C, F, G; 70A–C). The largest gracile forms are still septate at 150 mm diameter (table 9). These specimens are ornamented by distant, narrow prorsiradiate ribs with weak umbilical bullae, up to 26 per whorl, separated by broad interspaces that are smooth on molds. Most specimens only have inner ventrolateral clavi at this stage, while there are some specimens with clavi intercalated between the ribs or even short intercalated ribs. Riblets and striae form an acute chevron on the venter, while the keel remains minutely serrated when well preserved.

Robust forms have a much wider umbilicus and the whorl section varies from slightly compressed to depressed. In juveniles (fig. 67F–P) there are usually approximately 12 prominent umbilical bullae per whorl. These give rise to distant, narrow, rounded, straight, prorsiradiate primary ribs separated by wide interspaces, smooth on most molds. Bullae may be equal in strength or vary, while a few specimens have shorter intercalated ribs (fig.

Fig. 83. *Prionocyclus wyomingensis* Meek, ←

1876. USNM 7729D. This specimen bears the label 7729 in the same hand as the figured syntypes, and appears to be a previously unrecognized syntype, now paralectotype of the species. Middle Turonian *Scaphites warreni* Zone, Wall Creek Member of the Frontier Formation near Medicine Bow, Carbon County, Wyoming. Figure is ×0.9.

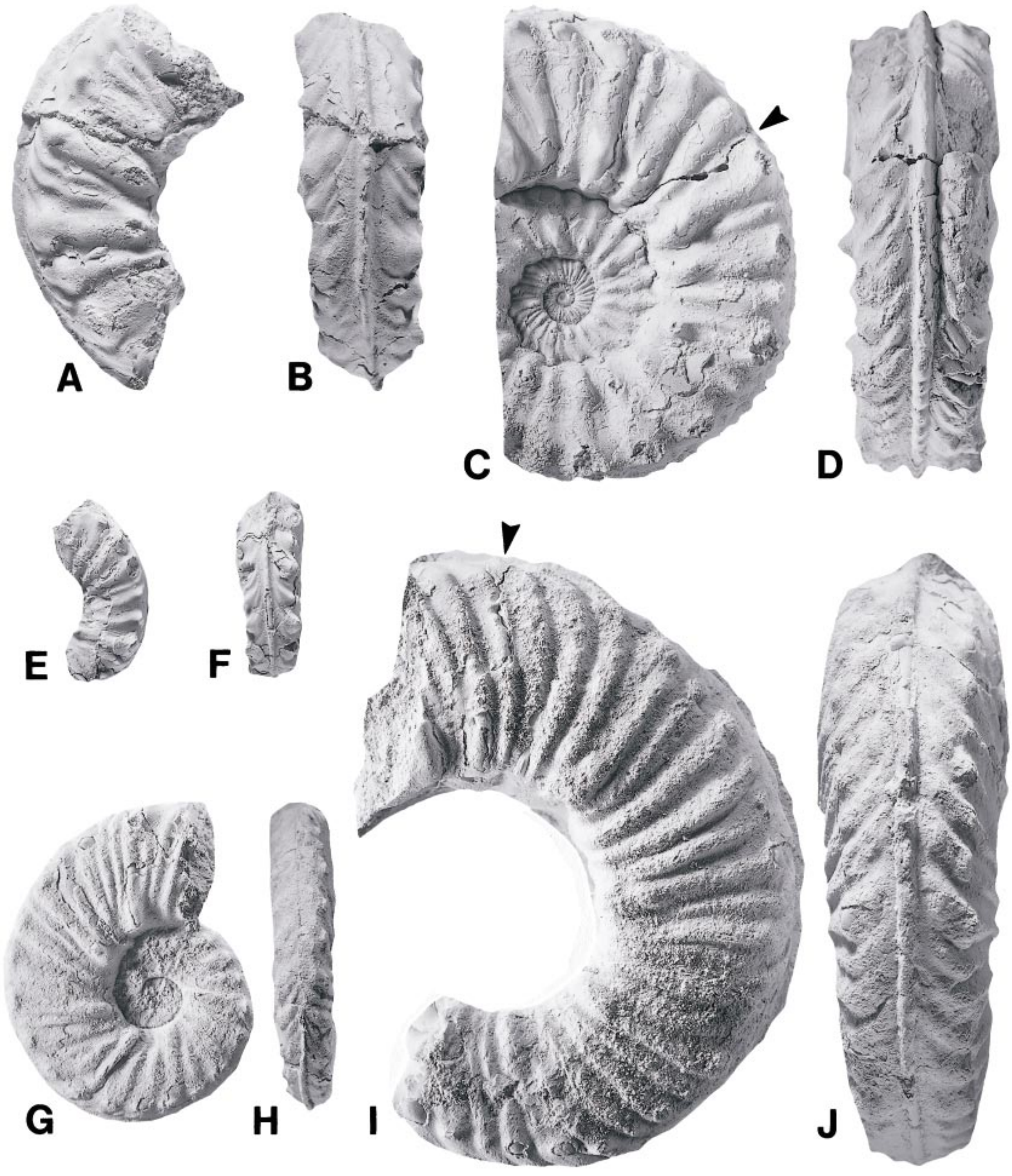


Fig. 84. *Prionocyclus wyomingensis* Meek, 1876. **A, B.** USNM 498411, robust form from locality 29. **C, D.** USNM 356921, robust form from locality 37. **E, F.** USNM 498412, robust form from locality 33. **G, H.** USNM 498413; **I, J.** USNM 498414, both gracile forms from locality 29. All figures are ×1.

69H, I). All ribs terminate in conical to feebly clavate inner ventrolateral tubercles, which may be equal or of variable strength. Broad ribs sweep forward to feeble outer ventrolateral clavi, which are lost early in middle growth. The ventral keel is entire and minutely serrated. If inner ventrolateral tubercles are strong, the umbilical seam and

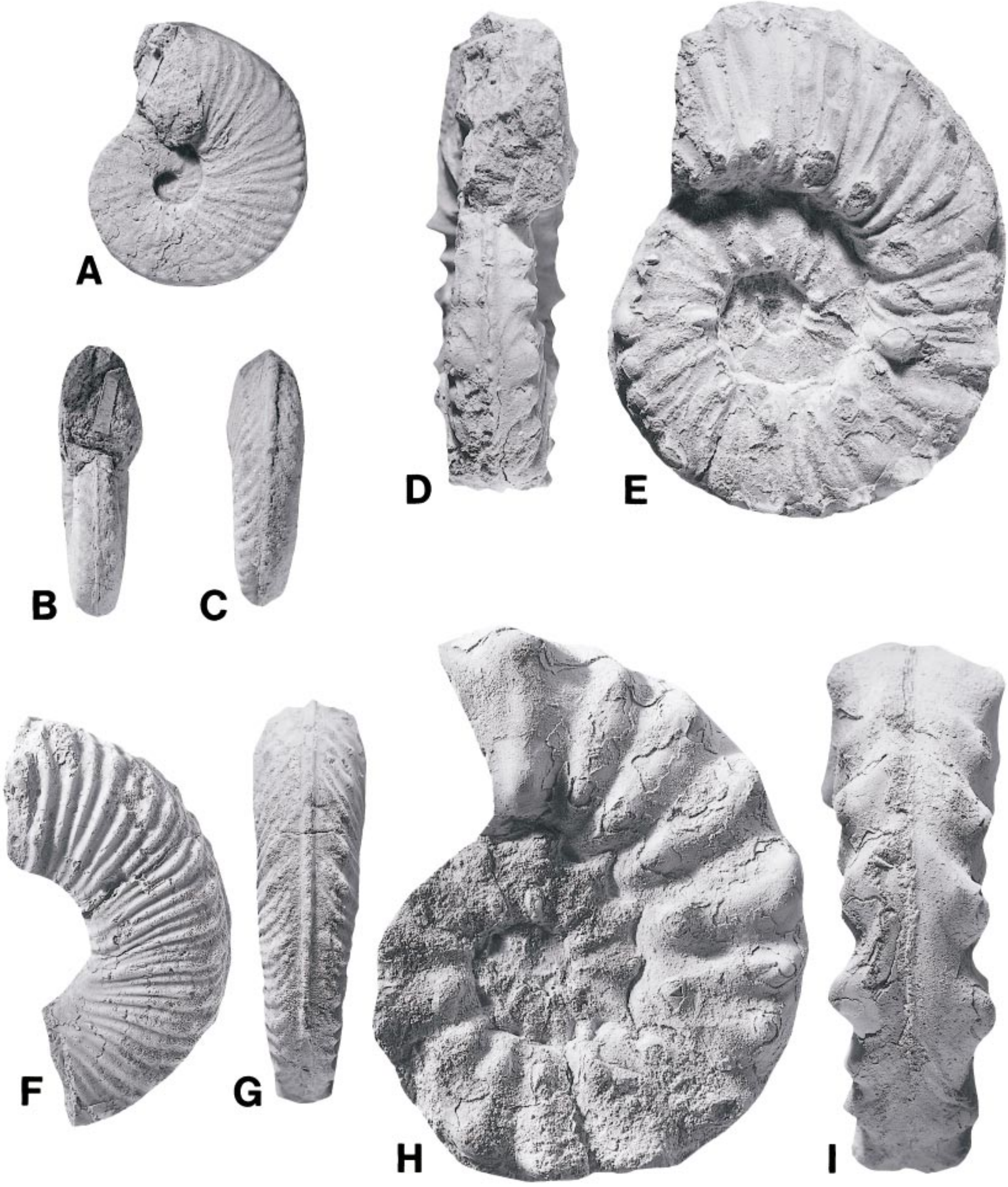


Fig. 85. *Prionocyclus wyomingensis* Meek, 1876. **A–C.** USNM 498403, gracile form from locality 28. **D, E.** USNM 498401, robust form from locality 28. **F, G.** USNM 498416, gracile form from locality 29. **H, I.** USNM 498402, robust form from locality 29. All figures are $\times$1.

wall of the succeeding whorl may be notched to accommodate them (fig. 69H). The venter is rounded or arched in early forms (fig. 68J–L), flattened in later ones (fig. 68F–I, O, P). As size increases, ornament may coarsen markedly, and a common variant has a depressed, polygonal coastal whorl section, strong conical umbilical bullae displaced out

Fig. 86. *Prionocyclus wyomingensis* Meek, 1876. Pathological specimen lacking keel. USNM 475903, *ex* J.I. Kirkland Collection, from the Juana Lopez Member of the Mancos Shale, in the SE$^{1}/_{4}$ sec. 4, T. 12S, R. 1E, Garfield County, Colorado. Figures are ×1.

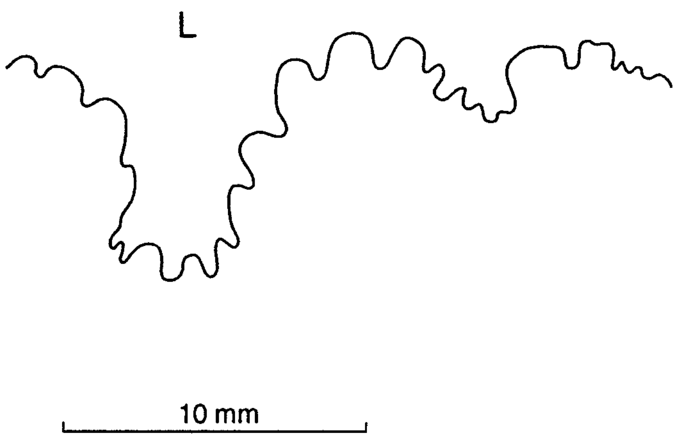


Fig. 87. External suture line of *Prionocyclus wyomingensis* Meek, 1876, USNM 498411, from locality 29.

TABLE 10
Dimensions of *Prionocyclus wyomingensis* Meek, 1876[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
Robust forms						
USNM 498401	Costal	63.3 (100)	21.8 (34.4)	21.5 (33.9)	1.01	23.0 (36.3)
	Intercostal	62.0 (100)	18.5 (29.8)	18.0 (29.0)	1.03	23.0 (37.1)
USNM 498402	Costal	83.7 (100)	30.2 (36.1)	30.8 (36.8)	0.98	32.3 (38.6)
	Intercostal	81.5 (100)	23.0 (28.2)	30.0 (36.8)	0.76	32.3 (39.6)
Gracile forms						
USNM 498403	Costal	40.2 (100)	12.2 (30.3)	15.5 (38.5)	0.79	10.4 (25.9)
USNM 498404	Costal	62.3 (100)	16.8 (27.0)	24.0 (38.5)	0.70	21.0 (33.7)
USNM 498405	Costal	137 (100)	34.2 (25.0)	50.6 (36.9)	0.68	50.8 (37.1)
	Intercostal	137 (100)	30.0 (21.9)	50.6 (36.9)	0.59	50.8 (37.1)
USNM 498406	Costal	168 (100)	51.3 (30.5)	60.0 (35.7)	0.86	64.7 (38.5)
	Intercostal	168 (100)	43.8 (26.1)	60.0 (35.7)	0.73	64.7 (38.5)
USNM 498407	Costal	198 (100)	61.4 (31.0)	69.0 (34.8)	0.89	85.0 (42.9)
	Intercostal	198 (100)	56.3 (28.4)	69.0 (34.8)	0.82	85.0 (42.9)
USNM 498408	Costal	228 (100)	58.3 (25.6)	75.5 (33.1)	0.77	95.0 (41.7)
	Intercostal	228 (100)	54.5 (23.9)	75.5 (33.1)	0.72	95.0 (41.7)

[a] See table 1 for explanation of symbols.

a little from the umbilical wall, low, broad, distant radial ribs, effaced at midflank, and blunt, conical inner ventrolateral horns. There may be low, blunt ventrolateral ribs with feeble tubercles between (figs. 72H, I). The keel commonly lacks regular serrations on the internal mold.

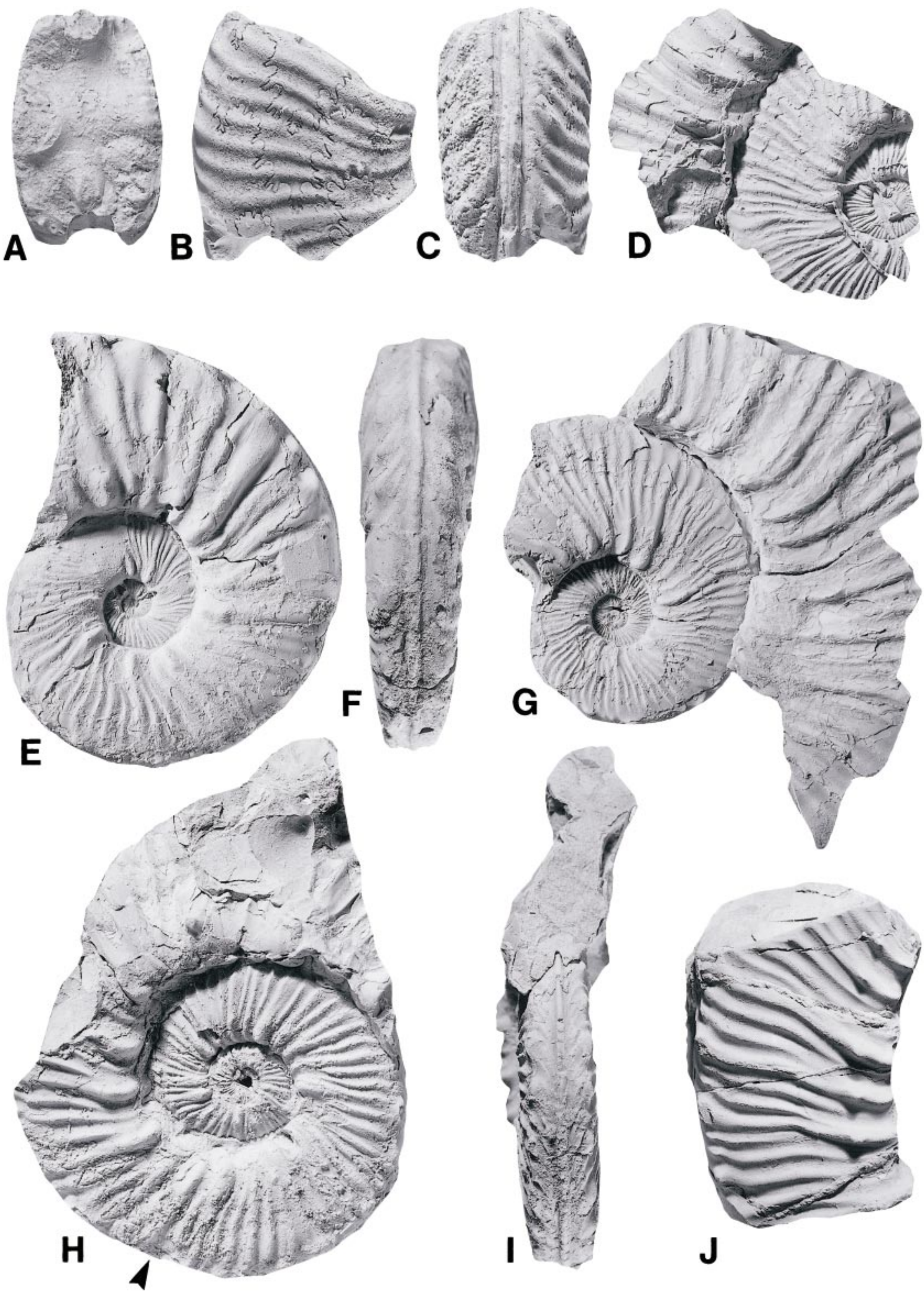
The largest fragments of the robust form are still septate at whorl heights of 70 mm, corresponding to an estimated diameter of 220 mm (table 9). Ornament consists of coarse, distant bituberculate ribs, the inner ventrolateral tubercles developing into sharp horns on molds, while there are occasional feeble intercalated ventrolateral tubercles. A body chamber fragment with a whorl height of 90 mm shows weakening umbilical bullae and a sharpening of ribs plus strong growth striae and lirae on the umbilical wall suggesting maturity at a size of 220–250 mm diameter. The fairly simple suture (fig. 74) has been illustrated by Meek (1876b: pl. 2, fig. 3c) and by Stanton (1894: pl. 41, fig. 3).

DISCUSSION: Differences between *Prionocyclus macombi* and *P. hyatti* are discussed above. *Prionocyclus bosquensis* Kennedy, 1988 (86, pl. 18, figs. 1–3, 10, 11; text-fig. 29a, d, f–i; figs. 76, 77), which is known only from crushed specimens, differs from *P. macombi* in showing bunching of ribs at umbilical bullae as well as persistence of inner and outer ventrolateral tubercles in middle growth. *P. wyomingensis* (figs. 78–87) is

TABLE 11
Dimensions of *Prionocyclus novimexicanus* (Marcou, 1858)[a]

Specimen	D	Wb	Wh	Wb:Wh	U
Robust forms					
USNM 498417	115.0 (100)	26.5 (23.0)	34.2 (29.7)	0.77	55.5 (48.3)
Gracile forms					
USNM 498418	51.8 (100)	13.0 (25.1)	24.9 (48.1)	0.52	14.5 (28.0)
USNM 498419	51.8 (100)	15.0 (29.0)	23.0 (44.4)	0.65	13.7 (26.4)
USNM 498420	60.0 (100)	17.7 (29.5)	25.3 (42.2)	0.70	17.9 (29.8)
USNM 498421	69.0 (100)	20.6 (29.9)	28.0 (40.6)	0.74	22.0 (31.9)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.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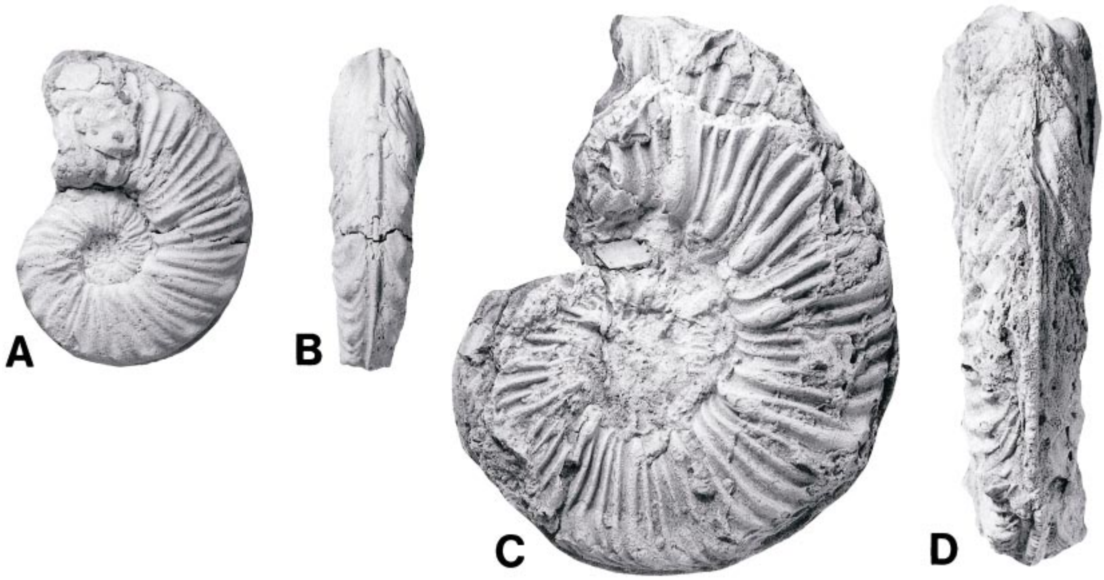

Fig. 89. *Prionocyclus novimexicanus* (Marcou, 1858). **A, B.** Holotype of *Prionocyclus wyomingensis elegans* Haas, 1946, the original of Whitfield, 1880, plate 14, figures 1, 2. **C, D.** Original of Whitfield, 1880, plate 14, figure 3. Both specimens are registered as USNM 12283, ''in silico-calcareous layers of Division No. 2, Cretaceous, on the east fork of Beaver Creek, near Camp Jenny, Black Hills.'' All figures are ×1.

known mostly from the gracile form, which exhibits much stronger, coarser ribbing than that of *P. macombi* with slender whorls. In addition, in *P. wyomingensis* the ribs sometimes arise in groups from bullae, and an inner lateral bulge or tubercle and a fingerlike septate horn on the inner ventrolateral tubercle develop at maturity.

OCCURRENCE: *Prionocyclus macombi* has been found in a wide belt paralleling the western shoreline of the basal late Turonian seaway that extends from western South Dakota southwestward to central Utah and then southeastward through most of New Mexico (fig. 75). The species is also known from north-central Texas.

Prionocyclus bosquensis Kennedy, 1988

Figures 76, 77

Prionocyclus bosquensis Kennedy, 1988: 86, pl. 18, figs. 1–3, 10, 11; text-figs. 29a, d, f–i.

Prionocyclus bosquensis Kennedy, 1988. Emerson et al., 1994: 212, 378.

TYPES: Holotype is OUM KT 3854 (fig. 76D); there are numerous paratypes of which the following are illustrated: OUM KT 3281 (fig. 76B), 3801b (fig. 76C), 3858 (fig. 76A), 3868 (fig. 77B), 3869 (fig. 76E), 3870 (fig. 77A), and 3873 (fig. 77C), from the top 6–7 m of the South Bosque Formation, Cement Works, 10 km (6 mi) southwest of Waco, McLennan County; also OUM KT 5375–85, pyritic juveniles from the same locality and

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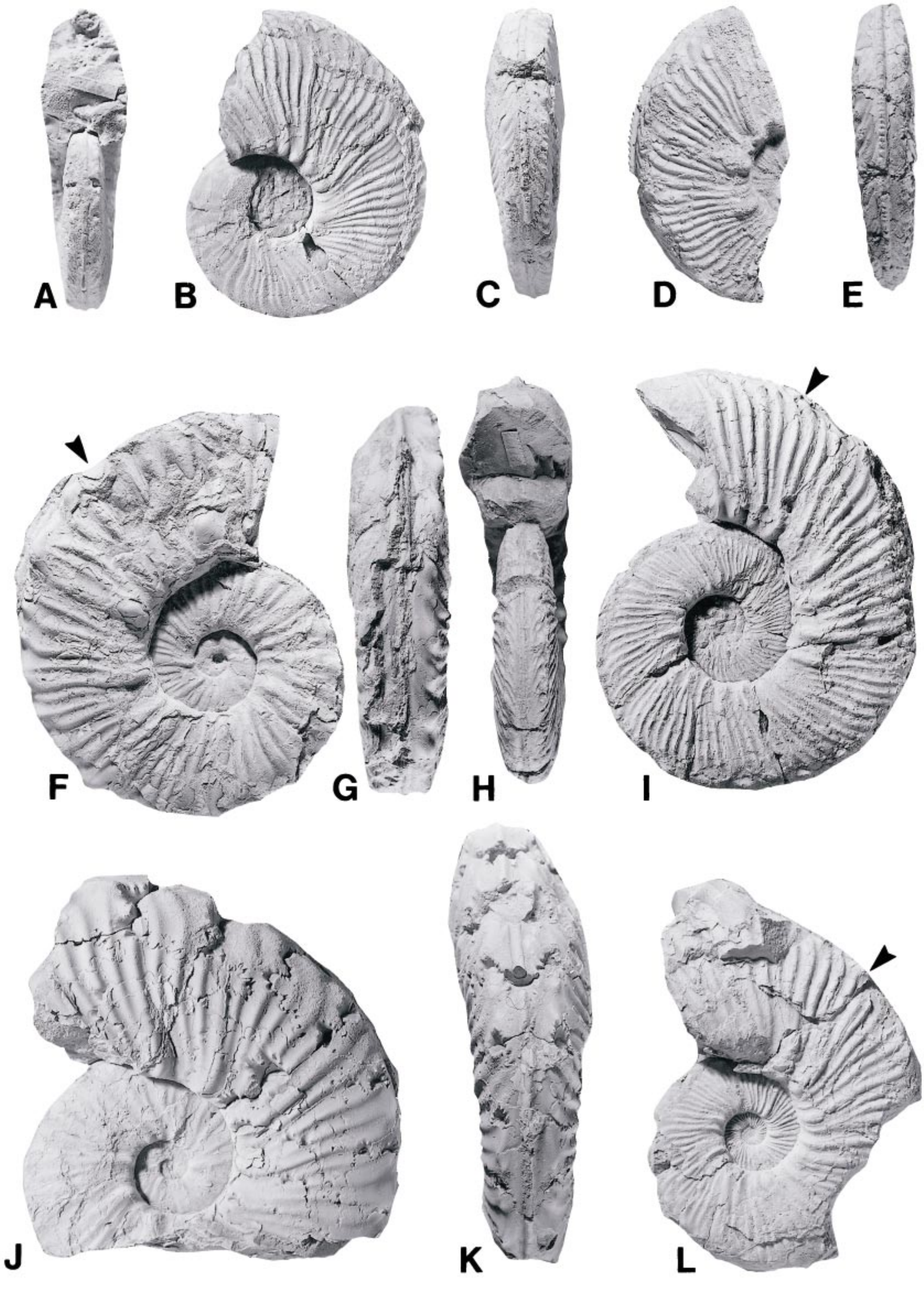
Fig. 88. *Prionocyclus novimexicanus* (Marcou, 1858). **A–C.** BMNH C49764, lectotype, a gracile form from either near Albuquerque, New Mexico, or La Lunes, New Mexico. **D.** USNM 498424, gracile form from locality 2. **E, F.** USNM 498421, gracile form from locality 1. **G.** USNM 498418, gracile form from locality 2. **H, I.** USNM 498425, gracile form from locality 1. **J.** USNM 498426, gracile form from locality 2. All figures are ×1.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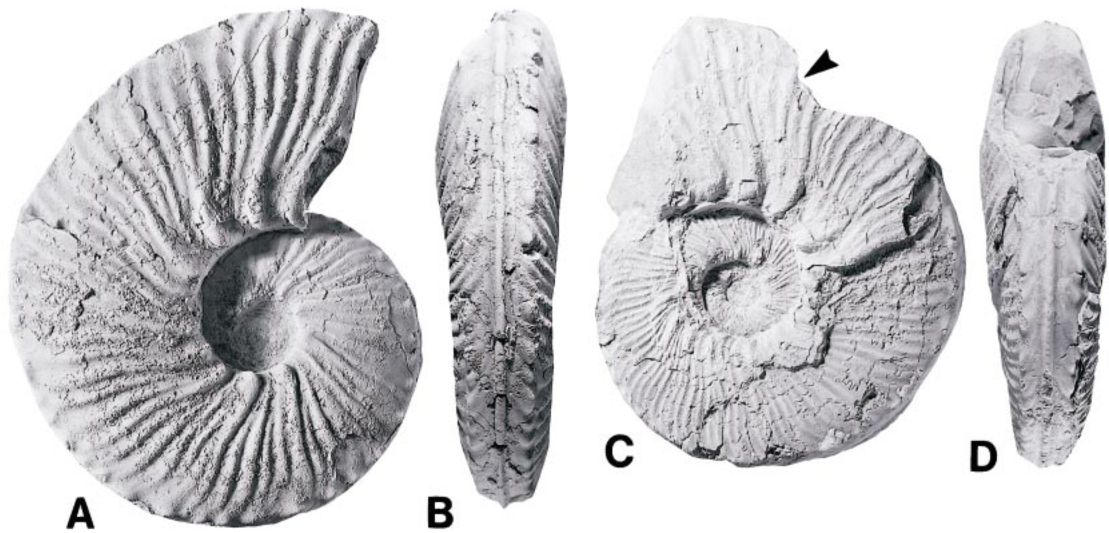

Fig. 91. *Prionocyclus novimexicanus* (Marcou, 1858). **A, B.** USNM 254556, gracile form from locality 13. **C, D.** USNM 498431, gracile form from locality 2. All figures are ×1.

horizon; OUM KT 5372a, b collected in situ 3 m below the base of the Austin Chalk at this locality; OUM KT 5373a, b from 1 m below the Austin Chalk; upper Turonian *Scaphites whitfieldi* zone.

DIAGNOSIS: A small densely ribbed species with a minutely notched keel. Ribs flexuous and not distinctly separated into primaries and secondaries.

DESCRIPTION: This species has been fully described by Kennedy (1988: 86, 87): ''Most specimens are 10–45 mm diameter, are crushed, and retain original aragonitic shell. Coiling is fairly involute, with U = 29%. Ornament is highly variable. At one extreme are very finely ornamented individuals. These have very dense, crowded, narrow, flexuous prorsiradiate ribs, every fifth to sixth strengthened, with a tiny umbilicolateral bulla, a bullate inner ventrolateral, and an obliquely placed outer ventrolateral tubercle. The intermediate ribs generally lack umbilical bullae, and have very faint or no inner and outer ventrolaterals. There is a strong, minutely serrated siphonal keel. A few specimens may even lack differentiated ribs and bear fine, even ornament, without tubercles; some individuals show groups of 3 or so ribs arising from a bulla while all specimens bear long intercalated ribs inserted on the inner flank. These specimens usually retain their outer ventrolateral tubercles. They are linked, by strengthening of tubercles and progressive decline of the weaker, feebly tuberculate ribs to much rarer individuals with distant ribs with umbilical bullae, strong inner and weak outer ventrolaterals, the interspaces with weak to obsolete flank ribs, but short intercalated ribs on the ventrolateral shoulders and venter. There are a few much larger fragments, with whorl heights of up to 53 mm. All of these show strong distant ribs with umbilical bullae, prominent inner ventrolateral spines or tubercles, weak, or no outer ventrolaterals, and groups of riblets and growth striae extending from the inner ventrolateral nodes towards the mid-venter. Between these ribs are much finer intercalated

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Fig. 90. *Prionocyclus novimexicanus* (Marcou, 1858). **A–C.** USNM 498419; **D, E.** USNM 498427, both from locality 2. **F, G.** USNM 498420, gracile form from locality 3. **H, I.** USNM 498428, gracile form from locality 2. **J, K.** USNM 498429, gracile form from locality 3. **L.** USNM 498430, gracile form from locality 2. All figures are ×1.

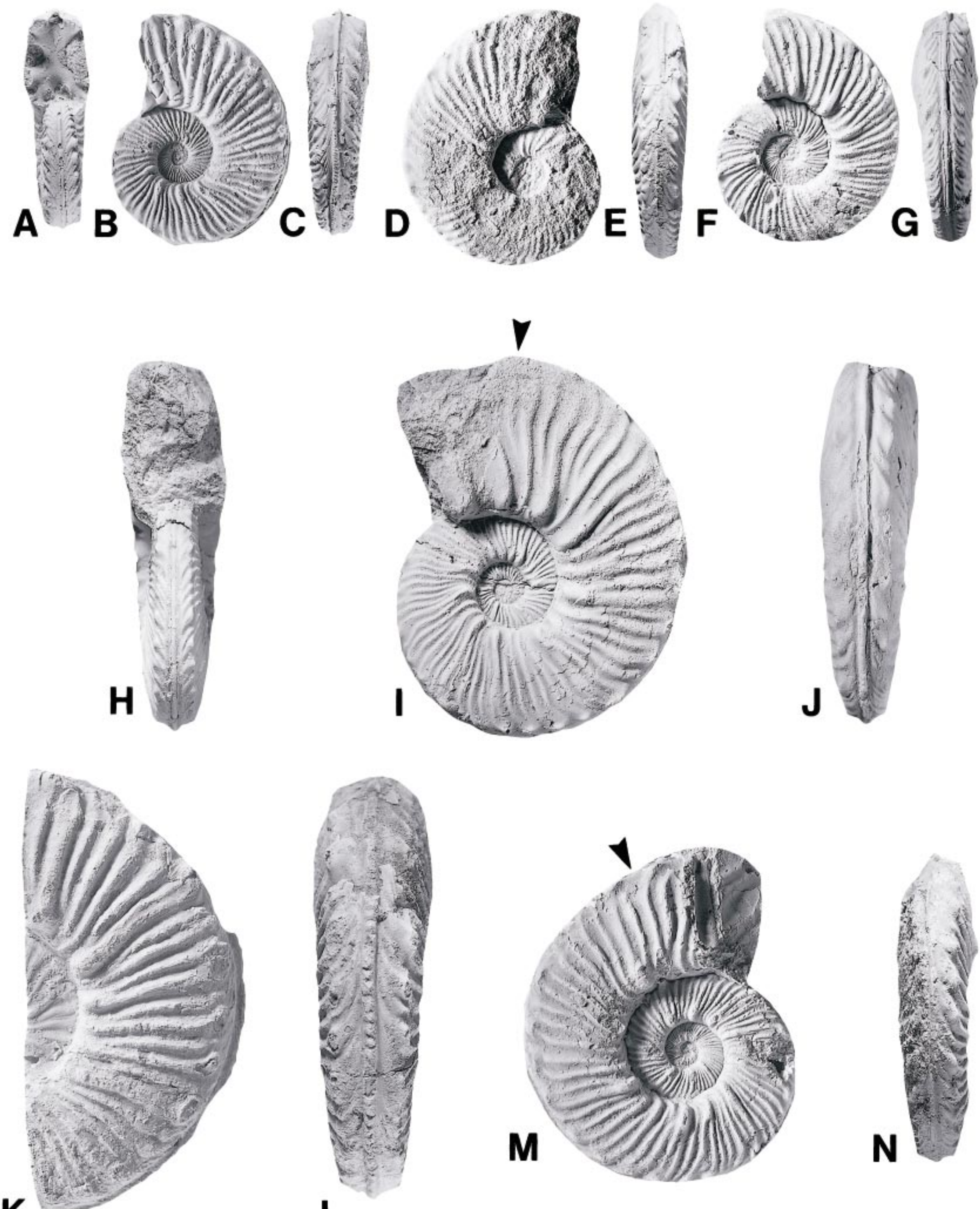


Fig. 92. *Prionocyclus novimexicanus* (Marcou, 1858). **A–C**. USNM 498432; **D, E**. USNM 498433; **F, G**. USNM 254555, all gracile forms from locality 13. **H–J**. USNM 498434, a gracile form from locality 24. **K, L**. USNM 498436, a gracile form from locality 31. **M, N**. USNM 498435, a gracile form from locality 13. All figures are ×1.

TABLE 12
Dimensions of *Prionocyclus germari* (Reuss, 1845)[a]

Specimen	Section	D	Wb	Wh	Wb:Wh	U
Robust forms						
USNM 498452	Costal	24.6 (100)	9.0 (36.6)	9.6 (39.0)	0.94	9.0 (36.6)
USNM 498453	Costal	31.5 (100)	10.9 (34.6)	12.0 (38.1)	0.91	11.2 (35.5)
USNM 498454	Costal	60.5 (100)	27.0 (44.6)	22.5 (37.2)	1.20	23.1 (38.2)
	Intercostal	60.5 (100)	23.5 (38.8)	22.5 (37.2)	1.04	23.1 (38.2)
USNM 498455	Costal	81.8 (100)	33.5 (38.3)	31.3 (38.2)	1.07	34.5 (42.2)
	Intercostal	81.8 (100)	29.0 (35.5)	31.3 (38.3)	0.93	34.5 (42.2)
USNM 498456	Costal	172 (100)	— (—)	58.0 (33.7)	—	77.2 (44.9)
Gracile forms						
USNM 498457	Costal	28.4 (100)	9.0 (31.7)	9.9 (34.9)	0.91	10.2 (35.9)
USNM 498458	Costal	40.3 (100)	11.5 (28.5)	17.4 (43.2)	0.66	14.3 (35.9)
USNM 498459	Costal	46.2 (100)	13.1 (28.4)	16.4 (35.5)	0.80	18.8 (40.7)
USNM 498460	Costal	58.5 (100)	16.5 (28.2)	21.9 (37.4)	0.75	22.5 (38.5)
USNM 498461	Costal	95.0 (100)	32.8 (34.5)	35.5 (37.4)	0.92	37.7 (39.7)

[a] See table 1 for explanation of symbols.

riblets and lirae. There is a strong crenulate siphonal keel. Sutures not seen."

DISCUSSION: See Kennedy (1988: 88).

OCCURRENCE: As for types.

Prionocyclus wyomingensis Meek, 1876

Figures 78–87

Ammonites serrato-carinatus Meek, 1870: 429.

Ammonites (*Pleuroceras?*) *serrato-carinatus* Meek, 1871: 298.

Prionocyclus wyomingensis Meek, 1876a: 452, footnote.

Prionocyclus wyomingensis Meek. White, 1880: 35, pl. 15, fig. 1a–e.

non Prionocyclus wyomingensis Meek. Whitfield, 1880: 440, pl. 14, figs. 1–3 (= *P. novimexicanus* (Marcou).

Prionocyclus wyomingensis Meek. White, 1883: 35, pl. 15, fig. 1a–e.

Prionocyclus wyomingensis Meek. Boyle, 1893: 243.

Prionocyclus wyomingensis Meek. Stanton, 1894: 171, pl. 40, figs. 1–4.

Prionocyclus wyomingensis Meek. Gilbert, 1896: 565, pl. 58, figs. 1–3.

Prionocyclus wyomingensis Meek. Logan, 1898: 463, pl. 106, figs. 1–4.

Prionocyclus wyomingensis Meek. Johnson, 1903: 139.

Prionocyclus wyomingensis Meek. Barbour, 1903: pl. 5, figs. 4, 5.

Prionocyclus wyomingensis Meek. Grabau and Shimer, 1910: 228, fig. 1510a–d.

Prionocyclus wyomingensis Meek. Diener, 1925: 155.

Prionocyclus reesidei Sidwell, 1932: 318 (*pars*), pl. 49, figs. 10, 11 only.

Prionocyclus wyomingensis Meek. Roman, 1938: 457, pl. 46, fig. 435.

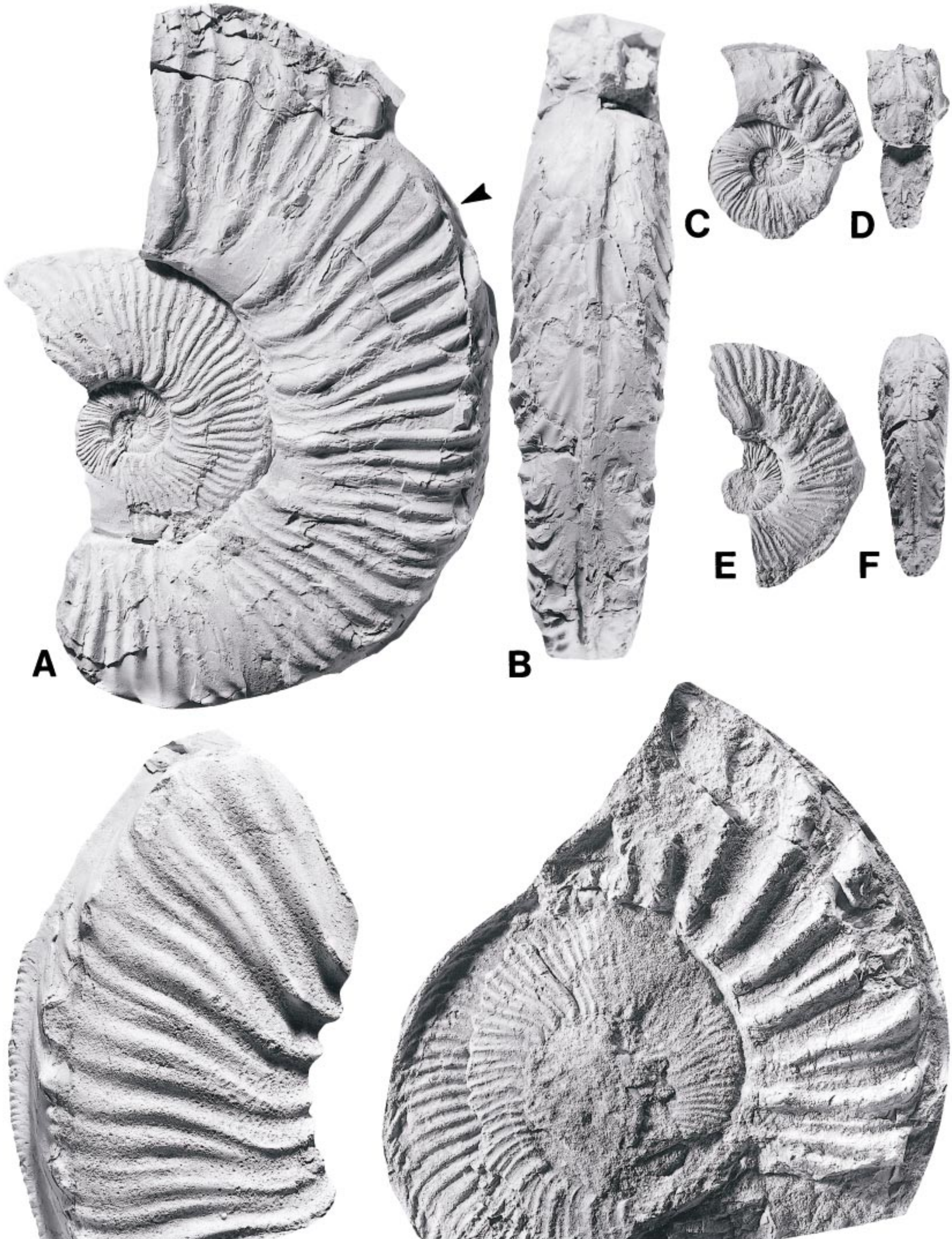
Prionocyclus wyomingensis Meek. Shimer and Shrock, 1944: 593, pl. 247, figs. 3, 4.

Prionocyclus wyomingensis Meek. Haas, 1946 and varieties *robusta* (p. 200), *non* var. *elegans* (p. 210) (= *P. novimexicanus*); pl. 18, figs. 3–6; *non* pl. 19, figs. 1–7, 11–14 (= *P. novimexicanus*); pl. 20, figs. 1–3, 5–7, *non* pl. 20, fig. 4 (= *P. novimexicanus*); pl. 22, figs. 3–5; *non* pl. 22, figs. 1, 2 (= *P. novimexicanus*); pl. 23, figs. 1, 3 (in part); pl. 24, figs. 2, 3; text-figs. 93–97, 105–108; *non* 98–104 (= *P. novimexicanus*).

TABLE 13
Dimensions of *Prionocyclites mite* Kennedy, 1988[a]

Specimen	D	Wb	Wh	Wb:Wh	U
USNM 420144	18.2 (100)	4.5 (24.7)	6.8 (37.4)	0.66	4.5 (26.4)

[a] See table 1 for explanation of symbols. All measurements are on costal sections.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Prionocyclus wyomingensis Meek. Wright, 1957: 426, fig. 547. 6a, 6b.
Prionocyclus wyomingensis Meek. Termier and Termier, 1960: fig. 2418.
Prionocyclus wyomingensis Meek. Matsumoto, 1965: 18, pl. 16, fig. 1a–c; pl. 17, fig. 2a–c; pl. 18, fig. 1a–c (? = *P. novimexicanus*).
Prionocyclus wyomingensis Meek. Matsumoto, 1971: 132, pl. 21, fig. 2; pl. 22, fig. 1, text-fig. 2.
Prionocyclus wyomingensis Meek. Hattin, 1975b: pl. 2, fig. 11.
Prionocyclus wyomingensis Meek. Kauffman, 1977: pl. 26, figs. 2, 3.
Prionocyclus wyomingensis Meek, 1876. Kennedy et al., 1989: 91, fig. 24E.
Prionocyclus wyomingensis Meek, 1876. Kennedy, 1988: 88, pl. 14, fig. 8.
Prionocyclus wyomingensis Meek, 1876. Hall et al., 1994: 305, figs. 4I, N, O, 5A–C, G–J.
Prionocyclus wyomingensis Meek. Emerson et al., 1994: 212, 378.
Prionocyclus wyomingensis Meek. Wright, 1996: 186, fig. 4a, b.
Prionocyclus wyomingensis Meek, 1876. Reyment and Kennedy, 2001: fig. 3.

TYPES: Lectotype, by the subsequent designation of Matsumoto, 1965: 18 is USNM 7729, the original of Stanton, 1894: plate 40, figure 3 (fig. 78); two paralectotypes have the same number and are the originals of Stanton, 1894: plate 40, figures 1, 2 (figs. 79, 80). A further probable unfigured paralectotype bears the number 7729D, and is shown in figures 82, 83. All are from what is now known as the Wall Creek Sandstone Member of the Frontier Formation in the Medicine Bow River valley of Southeast Wyoming (fide Cobban, 1984a: 86).

DIAGNOSIS: A large species for the genus; moderately evolute; keel notched into more siphonal clavi than ribs. Gracile form has closely spaced prorsiradiate primary and secondary ribs. Primary ribs bear lengthy umbilical bullae that may divide into shorter umbilical bullae and bullate or nodate inner lateral tubercles. All primaries bear nodate inner ventrolateral tubercles and weaker clavate to bullate outer ventrolateral tubercles. Robust form has coarse ribs that support prominent nodate umbilical tubercles, nodate inner ventrolateral tubercles, and weak outer ventrolateral clavi.

DESCRIPTION: The robust form is rare (figs. 84A–F, 85D, E, H, I). Coiling is evolute with U/D = 0.30–0.37 in the available material (table 10); the umbilicus broad, the umbilical wall flattened and inclined outward, with grooves to accommodate the inner ventrolateral spines of the preceding whorl (fig. 85E). The umbilical shoulder is narrowly rounded, the whorl section slightly compressed to slightly depressed, with the greatest breadth at the umbilical bullae costally and just outside the umbilical shoulder intercostally.

Ornament is highly variable. At one extreme are very coarsely ribbed individuals with only 16 or 17 ribs per whorl. Ribs arise at the umbilical seam and strengthen into massive conical umbilical bullae, broaden and are straight and prorsiradiate across the flanks, and develop massive septate inner ventrolateral spines that generally appear as large clavi on the mold when the spines have broken off. The rib profile is somewhat concave between bulla and spine (fig. 85H, I). Broad ribs sweep forward across the ventrolateral shoulder to outer ventrolateral clavi and a smooth zone separates them from the strong and minutely serrated siphonal keel.

At the other extreme (fig. 85D, E) are similarly proportioned individuals that have 17 sharp to spinose umbilical tubercles in middle growth, each of which gives rise to a strong concave to straight and rectiradiate adapical primary rib and a much weaker adapertural primary rib, which loop to a strong inner ventrolateral clavus/spine, the arrangement resembling a bow. Broad ribs sweep forward over the ventrolateral shoulder and connect to weaker outer ventrolateral clavi. Between the looped, bullate ribs are one or two nonbullate ribs that extend to the umbilical seam or arise on the inner flanks and

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Fig. 93. *Prionocyclus novimexicanus* (Marcou, 1858). **A, B**. USNM 498437, a gracile form from locality 2. **C, D**. USNM 498438, a gracile form from locality 3. **E, F**. USNM 498439, a gracile form from locality 3. **G.** USNM 498440, a gracile form from locality 18. **H**. USNM 498441, a gracile form from locality 25. All figures are ×1.

Fig. 94. *Prionocyclus novimexicanus* (Marcou, 1858). USNM 498422, a gracile form from locality 2. Reduced ×0.53. Original is 386 mm in diameter.

Fig. 95. *Prionocyclus novimexicanus* (Marcou, 1858). USNM 498422; see also figure 94. Reduced ×0.53. Original is 386 mm in diameter.

Fig. 96. *Prionocyclus novimexicanus* (Marcou, 1858). USNM 498423, robust form from locality 4. Reduced ×0.53. The original is 380 mm in diameter.

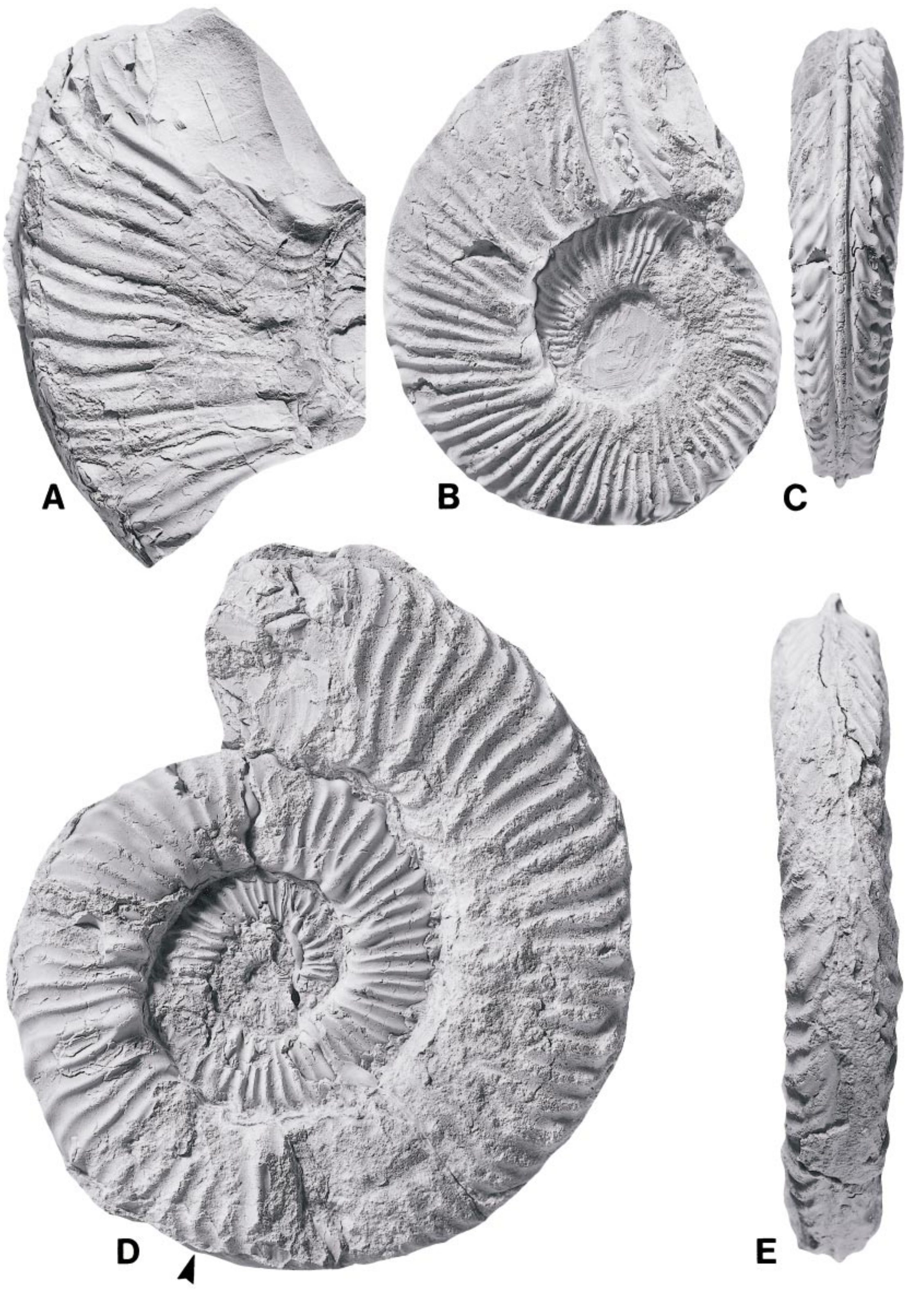
develop much weaker ventrolateral tubercles, the arrangement giving the shell a highly irregular ornament. The largest robust individual seen is 83 mm in diameter.

Gracile individuals are common (figs. 78–81; ?82, ?83; 84G–J, 85A–C, F, G). At 40 mm diameter, coiling is evolute, with U/D = 0.26 (table 10); the umbilicus is shallow, with a low flattened umbilical wall. The whorls are high and compressed (whorl breadth to height ratio averages 0.79), with fine, dense, crowded ribs. There are up to 12 weak umbilical bullae that give rise to single or paired ribs, with single nonbullate ribs between that extend to the umbilicus or not, yielding a total of 44–48 ribs per whorl. Ribs are crowded, flexuous, and prorsiradiate, with small bullate to clavate inner, and clavate outer ventrolateral tubercles.

In middle growth, specimens have up to 70 ribs per whorl. There are up to 18 bullae per whorl, initially at the umbilical shoulder, but tending to move out to the inner flanks, when a new bulla develops (fig. 81C). They are the bases of septate umbilical spines, and give rise to pairs of coarse ribs that are straight and prorsiradiate and initially loop to outer ventrolateral tubercles that are also the bases of septate spines. As size increases, the tendency to loop declines and the adapertural rib of the pair may detatch. There are one to six weaker, nonbullate long ribs between the bullate ones, each of which may develop a weak inner ventrolateral tubercle.

The ribs sweep forward over the ventrolateral shoulder to small, obliquely placed outer ventrolateral tubercles and form an acute chevron with the high and minutely serrated siphonal keel. The largest gracile individuals are 220–230 mm diameter. At maturity, the bullate ribs strengthen markedly and are very coarse, high, and barlike. Where well-preserved, they bear long inner lateral and inner ventrolateral spines, while sharp outer ventrolateral clavi are also present. Between are up to three much weaker, narrow, sharp long ribs that lack any trace of a tu-

Fig. 97. *Prionocyclus novimexicanus* (Marcou, 1858). USNM 498423, see also Figure 96. Reduced ×0.53. The original is 380 mm in diameter.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bercle. This coarseness and marked differentiation of the main ribs gives a highly characteristic appearance to the shell.

The largest collection studied consists of 73 specimens from the Frontier Formation at USGS Mesozoic locality D9244 in southeastern Wyoming. Of these specimens 61 are the gracile form and 12 are the robust form.

The suture is fairly simple and typical of the genus. The suture from White (1880) is shown here (fig. 87).

DISCUSSION: Differences between *P. wyomingensis, P. macombi,* and *P. bosquensis* are noted above. *P. wyomingensis* most closely resembles *P. novimexicanus* (Marcou, 1858) (figs. 88–101), which is presumably its descendant, but the latter is even more compressed, has flexuous ribs, seldom develops the umbilical and inner lateral tuberculation of *P. wyomingensis* and loses the outer ventrolateral tubercles at a very early stage so that the primary ribs are effectively bituberculate.

A remarkable pathological specimen (collected by J. I. Kirkland, Salt Lake City, Utah), USNM 475903 (fig. 86), from the Juana Lopez member of the Mancos Shale in the SE¼ sec. 4, T. 12 S, R. 1 E, Garfield County, Colorado, lacks a siphonal keel (fig. 86).

OCCURRENCE: *Prionocyclus wyomingensis* is widely distributed in the Western Interior of the United States from northwestern Montana south through much of New Mexico, and from east-central Utah to southwestern Kansas. It has also been figured recently from Alberta, Canada (Hall et al., 1994) and is known from Japan (Matsumoto, 1971).

Prionocyclus novimexicanus (Marcou, 1858)

Figures 88–101

Ammonites novi-mexicani Marcou, 1858: 35, pl. 1, fig. 2.
Prionocyclus wyomingensis Meek. Whitfield, 1880: 440, pl. 14, figs. 1–3.
Prionocyclus wyomingensis Meek var. *elegans* Haas, 1946: 200, pl. 19, figs. 1–7, 11–14; pl. 20, fig. 4; pl. 21, figs. 1–3, 5; pl. 22, figs. 1, 2; text-figs. 98–104.
Prionocyclus wyomingensis Meek. Luppov and Druschchits, 1958: 123, text-fig. 97b, pl. 60, fig. 3.
Prionocyclus (*Prionocyclus*) *wyomingensis* var. *elegans* Haas. Jeletzky, 1970: pl. 26, fig. 8.
Prionocyclus wyomingensis Meek. Kennedy and Cobban, 1976: pl. 11, fig. 4.
Prionocyclus wyomingensis elegans Haas. Kauffman, 1977: 260, pl. 22, fig. 14.
Prionocyclus novimexicanus (Marcou). Hook and Cobban, 1979: 38, fig. 3E–L.
Prionocyclus novimexicanus (Marcou). Merewether et al., 1979: pl. 3, fig. 3.
Prionocyclus wyomingensis Meek. Case, 1982: fig. 12. 63.
Prionocyclus novimexicanus (Marcou). Cobban, 1984b: 14, pl. 1, figs. 15, 16.
Prionocyclus novimexicanus (Marcou, 1853). Kennedy, 1988: 83.
Prionocyclus novimexicanus (Marcou, 1848). Kennedy et al., 1989: 93.
Prionocyclus novimexicanus (Marcou). Cobban and Hook, 1989: fig. 10j–l.
Prionocyclus novimexicanus (Marcou, 1858). Amédro, 1990: 269, pl. 17, fig. 6; pl. 25, figs. 1–3.
Prionocyclus novimexicanus (Marcou). Emerson et al., 1994: 212, 378.
Prionocyclus novimexicanus (Marcou, 1858). Reyment and Kennedy, 2001: fig 2i–m.

TYPES: The lectotype, here designated, of *Ammonites novimexicani* Marcou, 1858, is BMNH C49764 (fig. 88A–C), either from near Albuquerque, New Mexico, or La Lunes, New Mexico. Marcou specifically mentions two specimens in his account, and lectotype designation is necessary. The holotype of *Prionocyclus wyomingensis elegans* Haas, 1946 (a synonym), is the original of Whitefield, 1880: plate 14, figure 2, from Beaver Creek, near Camp Jenney, South Dakota, USNM 12283 (fig. 89A, B).

DIAGNOSIS: This large, moderately evolute species has a keel notched into small siphonal tubercles more numerous than the ribs. The gracile form has dense, flexuous primary

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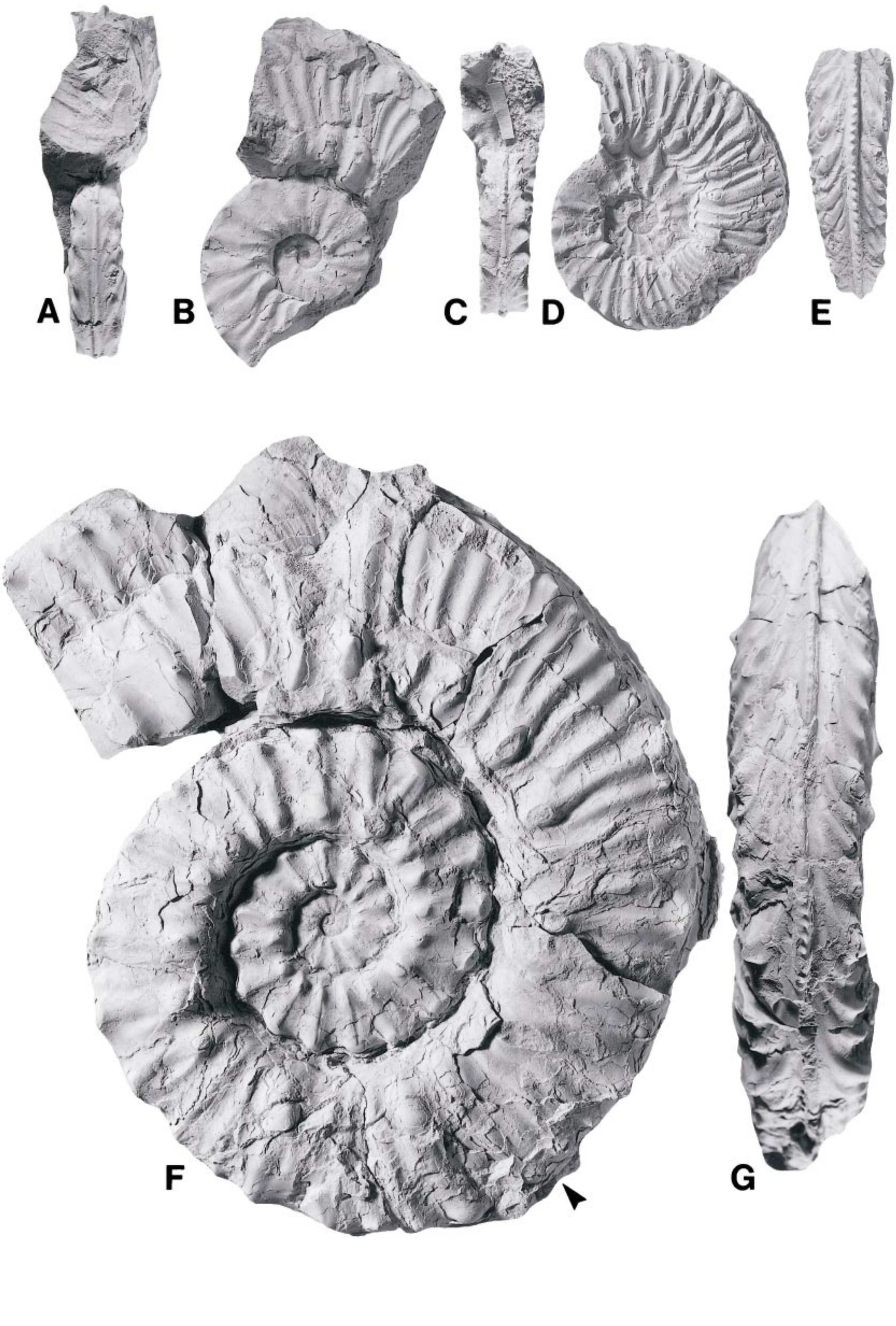
Fig. 98. *Prionocyclus novimexicanus* (Marcou, 1858). **A**. USNM 498442, a gracile form from locality 2. **B, C**. USNM 498443, a gracile form from locality 9. **D, E**. USNM 498444, a robust form from locality 10. All figures are ×1.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and secondary ribs. Primary ribs arise from elongated umbilical bullae, each of which is rarely divided into a shorter umbilical bulla and a small, nodate inner lateral tubercle. All primaries bear rounded to clavate inner ventrolateral tubercles. Outer ventrolateral tubercles are usually absent, and very weak if present. The robust form is more evolute and more sparsely ribbed. Looped ribs may connect umbilical and inner ventrolateral tubercles in both gracile and robust forms.

DESCRIPTION: The best example of the robust form is USNM 498417 (fig. 99F, G). Coiling is very evolute, with U/D = 0.48, the umbilical wall flattened and inclined outward, the umbilical shoulder broadly rounded, the flanks convergent with the greatest breadth at the umbilical shoulder intercostally and at the umbilical bulla in costal section. The whorl section is compressed, with a costal whorl breadth to height ratio of 0.73 up to a shell diameter of 60 mm (table 11). Ornament consists of blunt umbilical bullae, 18 per whorl. These give rise to broad, low, straight prorsiradiate ribs that weaken markedly at midflank, and connect to blunt inner ventrolateral bullae. Broad ribs sweep forward and decline, forming an acute chevron with the minutely serrated siphonal keel; there is no trace of an outer ventrolateral tubercle. Beyond 60 mm, the bullae weaken progressively, and commonly give rise to pairs of ribs, which may loop to the inner ventrolateral bullae (fig. 100C, D) or not. Between are one or two weaker nonbullate ribs, arising at the umbilical shoulder or low on the flanks with feeble inner ventrolateral tubercles or not. The ribs become feebly flexuous at this stage.

The gracile form is represented by numerous specimens (figs. 88–95, 98A–C). Coiling is moderately evolute, with a shallow umbilicus with U/D = 0.26–0.30 between 50 and 100 mm shell diameter; the umbilicus is shallow, with a flattened wall. The whorl section is compressed, with whorl breadth to height ratios of 0.5–0.7 (table 11), the greatest breadth at the umbilical bullae in costal section and just outside the umbilical shoulder intercostally.

The earliest growth stages seen are characterized by very fine, dense, crowded ornament. Feeble umbilical bullae give rise to pairs or groups of three ribs; between are up to nine ribs which arise at the umbilical shoulder, low, or high on the flanks. The degree of differentiation between strong and bullate and weak and nonbullate ribs varies greatly between individuals (figs. 90–92), with up to 90 ribs per whorl. In middle growth, to a diameter of 70–80 mm, ribbing varies greatly in strength and density between individuals (compare fig. 90L and fig. 99A, B). Typically, there are 14–18 bullae per whorl that give rise to pairs or groups of ribs, with nonbullate intercalaries between, the bullate ribs looping in pairs to inner ventrolateral clavi, the nonbullate ribs with feeble inner ventrolateral tubercles or not. Feeble outer ventrolateral tubercles are present only at diameters of less than 15–20 mm. Beyond, ribs sweep forward over the ventrolateral shoulder to form an acute chevron. The siphonal keel is high, strong, and minutely serrated.

An adult of the gracile form has a maximum diameter of 386 mm (figs. 94, 95). It retains the crowded ornament of ribs of varying strengths to a diameter of 170 mm, beyond which the minor ribs decline progressively so that by the middle section of the body chamber, ornament consists of very distant, coarse, convex prorsiradiate ribs with strong, subspinose umbilical bullae and enormous, slender septate inner ventrolateral horns that persist to the last section of the body chamber. Just before the adult aperture, ribbing stops and the last section is covered in dense irregular riblets, lirae, and striae.

USNM 498423 (figs. 96, 97) is an uncrushed body chamber mold. The whorl height is 98 mm at the end of the phragmocone, and the diameter of the specimen is 380 mm, which suggests a total diameter of

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Fig. 99. *Prionocyclus novimexicanus* (Marcou, 1858). **A, B**. USNM 498445, a robust form from locality 2. **C–E**. USNM 498446, a robust form from locality 30. **F, G**. USNM 498417, a robust form from locality 1. All figures are ×1.

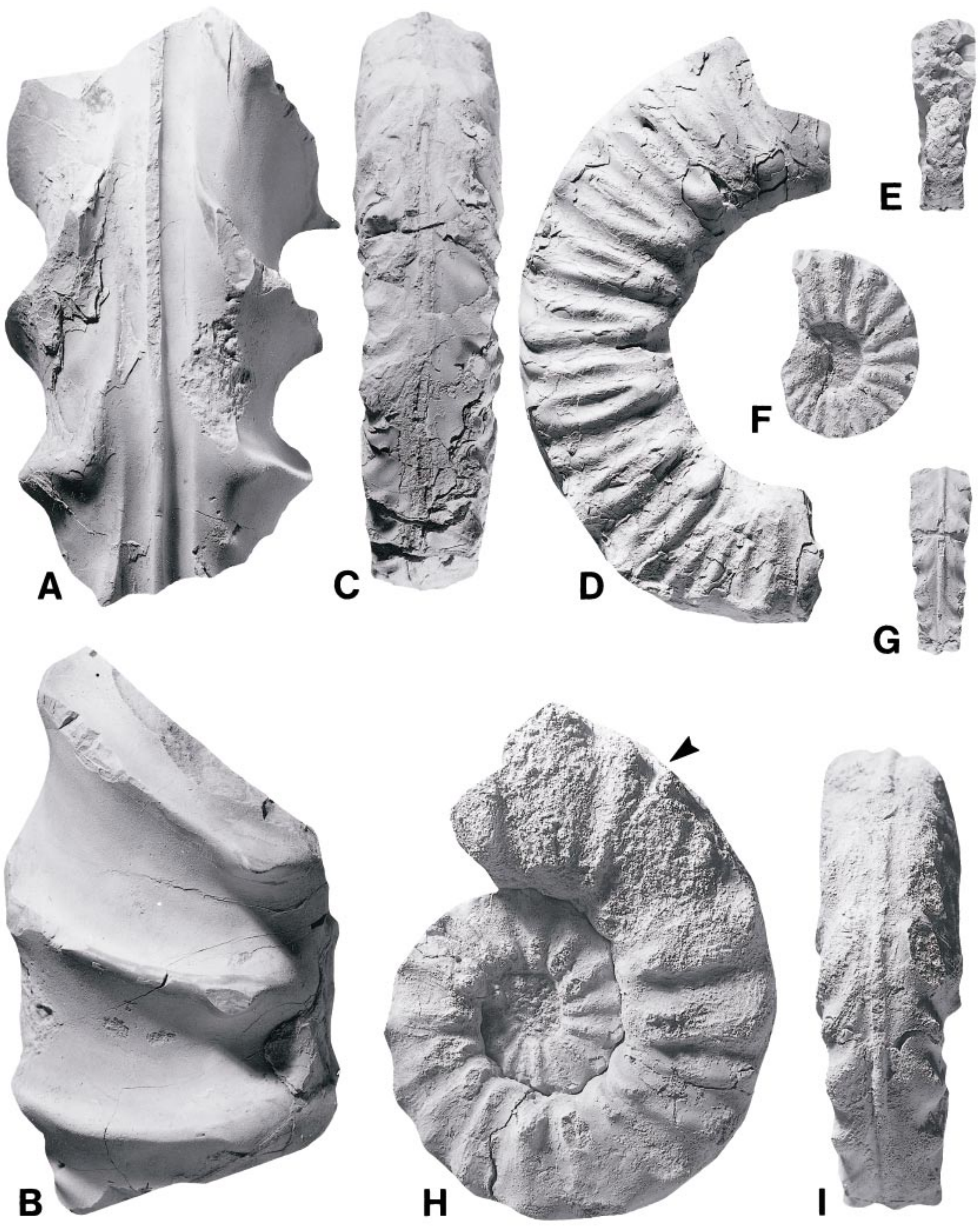


Fig. 100. *Prionocyclus novimexicanus* (Marcou, 1858). **A, B**. USNM 498447, a robust form from locality 2. **C, D**. USNM 498448, a robust form from locality 3. **E–G**. USNM 498449; **H, I.** USNM 498450, both robust forms from locality 31. All figures are ×1.

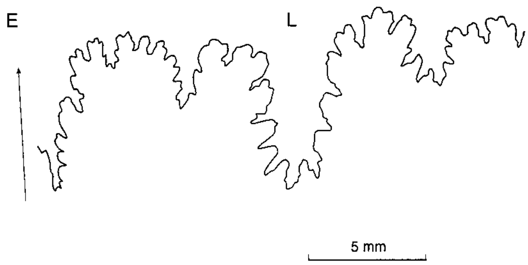


Fig. 101. External suture of *Prionocyclus novimexicanus* (Marcou, 1858). Copy of Haas, 1946, figure 104.

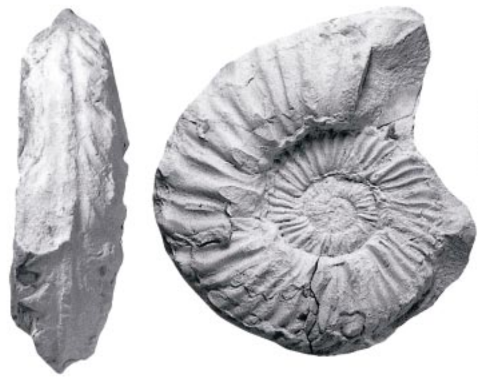


Fig. 102. *Prionocyclus quadratus* Cobban, 1953. Paratype USNM 108334, Sage Breaks Member of the Carlile Shale, 14.9 km (9 mi) south-southeast of Rapid City, in the NE¼ sec. 22, T. 1S, R. 8W, Pennington County, South Dakota. Figure is ×1.

over 400 mm. The whorl section at the end of the phragmocone is trapezoidal with a whorl breadth to height ratio of 0.95. Ornament consists of strong, distant, coarse primary ribs, with umbilical bullae that decline in strength as size increases. There are massive conical inner ventrolateral tubercles at the end of the phragmocone and beginning of the body chamber. They weaken on the later part of the body chamber. Narrow ribs project forward over the venter to form a chevron, with finer and irregular riblets between. The siphonal keel is blunt on the mold, and irregularly notched.

The suture has a broad, bifid E/L, narrow L, and bifid L/U_2 (fig. 101).

DISCUSSION: *Prionocyclus novimexicanus* most closely resembles its presumed ancestor, *P. wyomingensis* (figs. 78–87); differences are discussed above. *Prionocyclus quadratus* (figs. 102–107) and *P. germari* (figs. 109–119) never show the marked differentiation of rib strength of juvenile *P. novimexicanus*; instead the ribbing is even. The whorls are never as depressed or as finely ribbed, although *P. quadratus* and *P. germari* lose their outer ventrolateral clavi at very small diameters, as does *P. novimexicanus*. *Prionocyclus quadratus* develops a pronounced outer lateral bulge when adult (figs. 116–118), while the umbilical bullae commonly migrate out to an inner flank position in middle and late growth.

OCCURRENCE: Widely distributed in the Western Interior in the upper Turonian Zone of *Scaphites whitfieldi*. Specimens have been found in south-central and southeastern Montana, central and eastern Wyoming, western South Dakota, eastern Utah, and over much of Colorado and New Mexico. It has also been recorded from Trans-Pecos Texas (Kennedy et al., 1989), and Tunisia (Amédro, 1990).

Prionocyclus quadratus Cobban, 1953

Figures 102–107

Prionocyclus reesidei Sidwell, 1932: 354 (*pars.*), pl. 49, fig. 12 only.
Prionocyclus quadratus Cobban, 1953: 354, pl. 48, figs. 1–8.
Prionocyclus reesidei Sidwell. Kauffman, 1977: 260, pl. 2, figs. 2, 3.
Prionocyclus quadratus Cobban. Kauffman, 1977: 256, pl. 19, figs. 11, 12; pl. 26, fig. 1.
non Prionocyclus quadratus Cobban. Merewether et al., 1979: pl. 3, figs. 6–8 (= *P. germari*).
Prionocyclus quadratus Cobban, 1953. Kennedy, 1988: 83.
Prionocyclus quadratus Cobban. Cobban and Hook, 1989, fig. 10H, I.

TYPES: Holotype is USNM 108332 (fig. 103), paratypes USNM 108333a–c (figs. 104–106), from the upper Turonian Sage Breaks Member of the Carlile Shale in sec. 33, T. 9 S, R. 61 E, Carter County, Montana. Paratype USNM 108334 (fig. 102) is from a septarian concretion bed 12.8 m above the base of the Sage Breaks Member 14.5 km south-southeast of Rapid City in the NE¼ sec. 22, T. 1 S, R. 8 W, Pennington County, South Dakota. Paratype USNM 108335 is from a septarian concretion bed

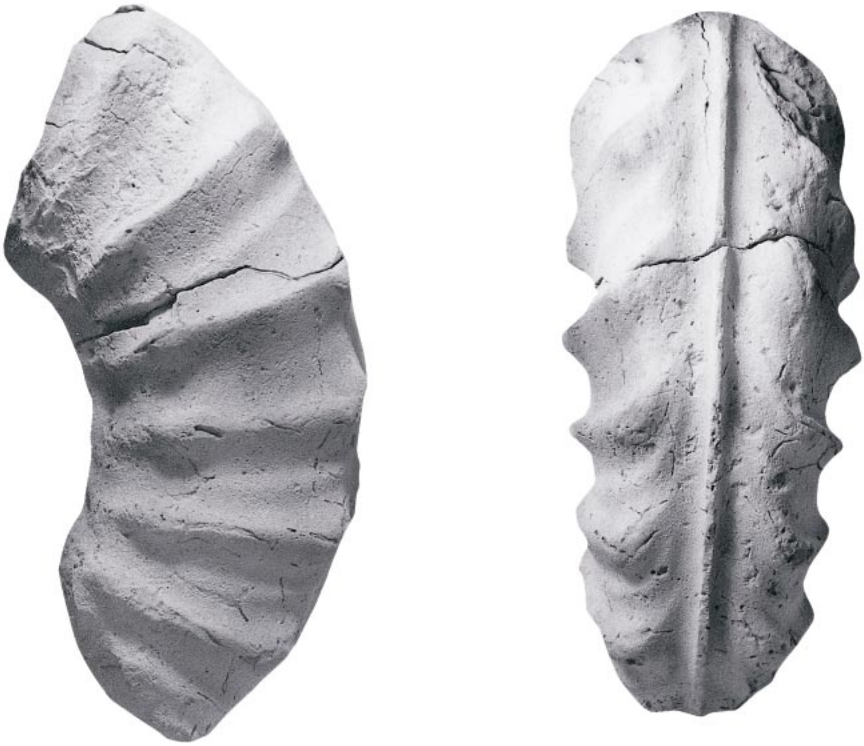


Fig. 103. *Prionocyclus quadratus* Cobban, 1953. Holotype, USNM 108332, Sage Breaks Member of the Carlile Shale, sec. 63, T 9S, R 61E, Carter County, Montana. Figures are ×1.

5.2 m below the top of the Turner Sandy Member of the Carlile Shale 10.4 km north of Belle Fourche, in the E½ sec. 2, T. 9 N, R. 2 E, Butte County, South Dakota.

DIAGNOSIS: A fairly large species that has sparsely ribbed adult whorls with strong primary ribs and weak secondary ribs. Primary ribs on the robust form have umbilical bullae, nodate inner ventrolateral tubercles, and midflank swellings or weak tubercles. The gracile form usually lacks midflank swellings. No clearly defined outer ventrolateral tubercles occur on either form.

DESCRIPTION: The types represent the robust form of the species. The holotype, USNM 108332 (fig. 103), is part of a small adult body chamber that has an intercostal width of 32.5 mm and height of 34.3 mm (ratio = 0.95) and a costal width of 42.0 mm and height of 38.2 mm (ratio = 1.10), with the greatest width at the umbilical shoulder. The specimen is an internal mold that does not have serrations on the keel preserved. A smooth ventral groove bounds the keel. Ribbing consists of strong, narrow, prorsiradiate primaries alternating with very weak, narrow secondaries. All ribs are straight on crossing the flanks, but they bend sharply forward on the ventrolateral shoulder and fade out on the venter. Primary ribs support umbilical bullae, weak midflank bullae, and blunt ventrolateral tubercles. Secondary ribs arise low on the flanks and efface on the venter without developing into ventrolateral tubercles.

A paratype, USNM 108334 (fig. 102), about 43 mm in diameter, has 42 ribs per whorl at a diameter of 30 mm with two or three secondaries separating primaries. At a larger diameter, most primaries are separated by a single secondary.

The suture figured by Cobban (1953: pl. 48, fig. 4) has a rather long lateral lobe, and a similar feature is shown in figure 107.

DISCUSSION: The species attains a large size, with some phragmocones having diameters of as much as 250 mm. Large specimens occasionally have blunt, nodate mid-

Fig. 104. *Prionocyclus quadratus* Cobban, 1953. Paratype, USNM 108333c, Sage Breaks Member of the Carlile Shale, sec. 63, T 9S, R 61E, Carter County, Montana. Figures are ×1.

flank tubercles. Keels are notched with more serrations than ribs.

The bulk of the specimens at hand represent the robust form. The gracile form tends to be more densely ribbed and lacks midflank swellings or bullae. Outer ventrolateral tubercles seem to be absent on both robust and gracile forms.

OCCURRENCE: Upper Turonian *Scaphites nigricollensis* and *S. corvensis* zones of the northern Great Plains of south-central and southeastern Montana and western South Dakota, and in equivalent strata in west-central New Mexico.

Prionocyclus germari (Reuss, 1845)

Figures 108A, B, D–F; 109–119

Ammonites Germari Reuss, 1845: 22, pl. 7, fig. 10.

Ammonites Germari Reuss. Schlüter, 1872: 41, pl. 11, figs. 15–17.

Ammonites Germari Reuss. Fritsch, 1872: 29, pl. 14, figs. 1, 2; pl. 16, fig. 7.

Ammonites Schlönbachi Fritsch, 1872: 33, pl. 16, fig. 5.

Schlönbachia Germari Reuss. Fritsch, 1893: 74, fig. 50.

Germariceras germari (Reuss). Breistroffer, 1947: unpaginated.

Germariceras germari (Reuss). Wright, 1957: L427, fig. 547.2.

Prionocyclus carvaholi Howarth, 1966: 224, pl. 1, figs. 8–11; pl. 2, figs. 3–6.

Prionocyclus quadratus Cobban. Scott et al., 1986: fig. 6K.

Prionocyclus germari (Reuss). Kaplan, 1988: 14, pl. 3, figs. 1–3, pl. 6, fig. 1.

Prionocyclus ?germari Reuss. Hall et al., 1994: 307, fig. 4J–L.

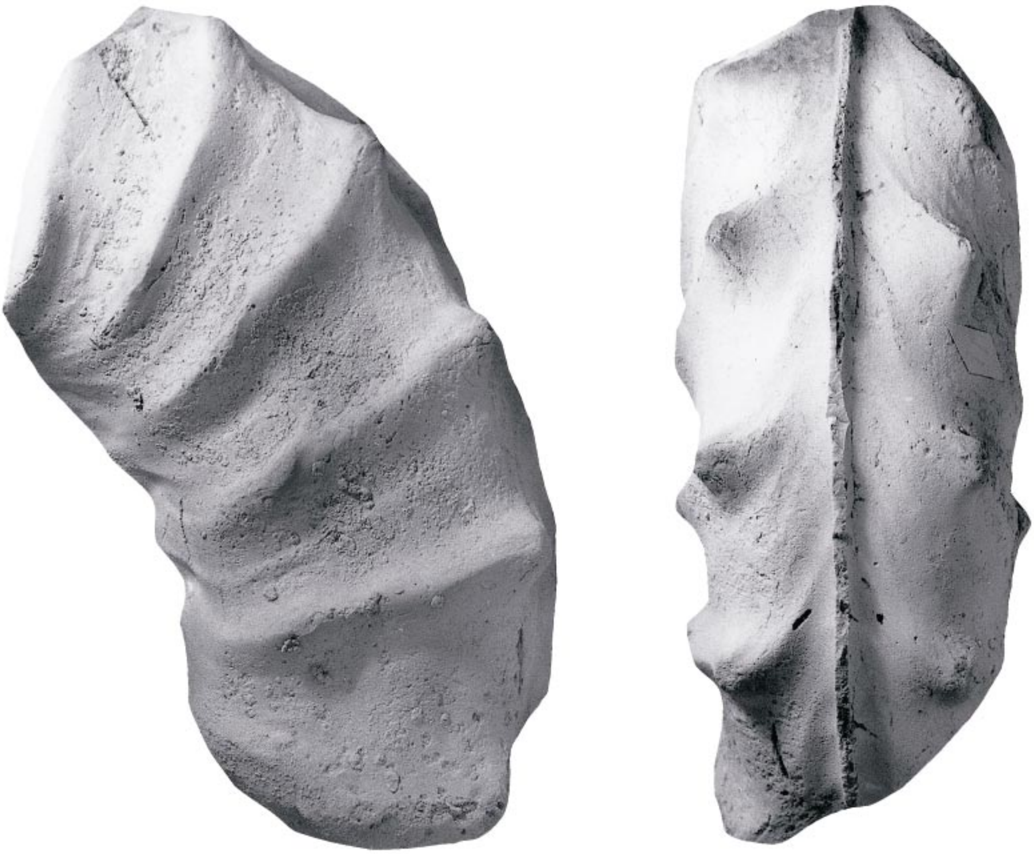


Fig. 105. *Prionocyclus quadratus* Cobban, 1953. Paratype, USNM 108333b, Sage Breaks Member of the Carlile Shale, sec. 63, T 9S, R 61E, Carter County, Montana. Figures are ×1.

Germariceras germari (Reuss, 1845). Wright, 1996: 186, fig. 142. 1a–c.
Prionocyclus germari (Reuss). Wiese, 1997: fig. 7.4.
Prionocyclus germari (Reuss, 1845). Kaczsrowski, 2000: 244, fig. 3a.
Prionocyclus germari (Reuss, 1845). Reyment and Kennedy, 2001: fig. 2.

TYPE: The lectotype, here designated, is the original of Reuss, 1845: 22, plate 7, figure 10, from the ''Planermergel von Werschowitz.'' The original figure is reproduced here as figure 109K.

DIAGNOSIS: Moderately to rather widely spaced, generally rounded, prorsiradiate ribs on the outer whorls characterize this species. Primary and secondary ribs tend to be of nearly uniform height. The keel is finely notched with many more serrations than ribs. The robust form has ribs that support bullate to nodate umbilical tubercles and nodate to clavate inner ventrolateral tubercles; weak outer ventrolateral clavi are present on some juveniles. The gracile form is weakly ribbed.

DESCRIPTION: Robust and gracile forms can be recognized starting from very small diameters. In the juvenile robust form (fig. 113A–P, T, U), the coiling is fairly evolute, with the umbilical wall notched to accommodate the inner ventrolateral nodes of the preceding whorl; the umbilicus represents 36–38% of the diameter (table 12) with a flattened wall and broadly rounded umbilical shoulder. The intercostal whorl section is slightly compressed with the greatest breadth just outside the umbilical shoulder; the costal section is polygonal with the greatest breadth at the umbilical bullae. There are 16–24 ribs per whorl between 25 and 60 mm in most specimens. The ribs arise at the umbilical

Fig. 106. *Prionocyclus quadratus* Cobban, 1953. Paratype, USNM 108333a, Sage Breaks Member of the Carlile Shale, sec. 63, T. 9S, R. 61E, Carter County, Montana. Figures are ×1.

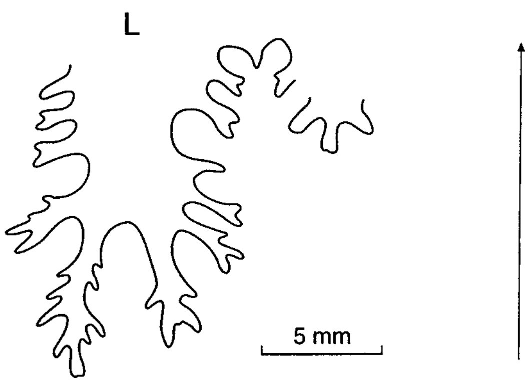
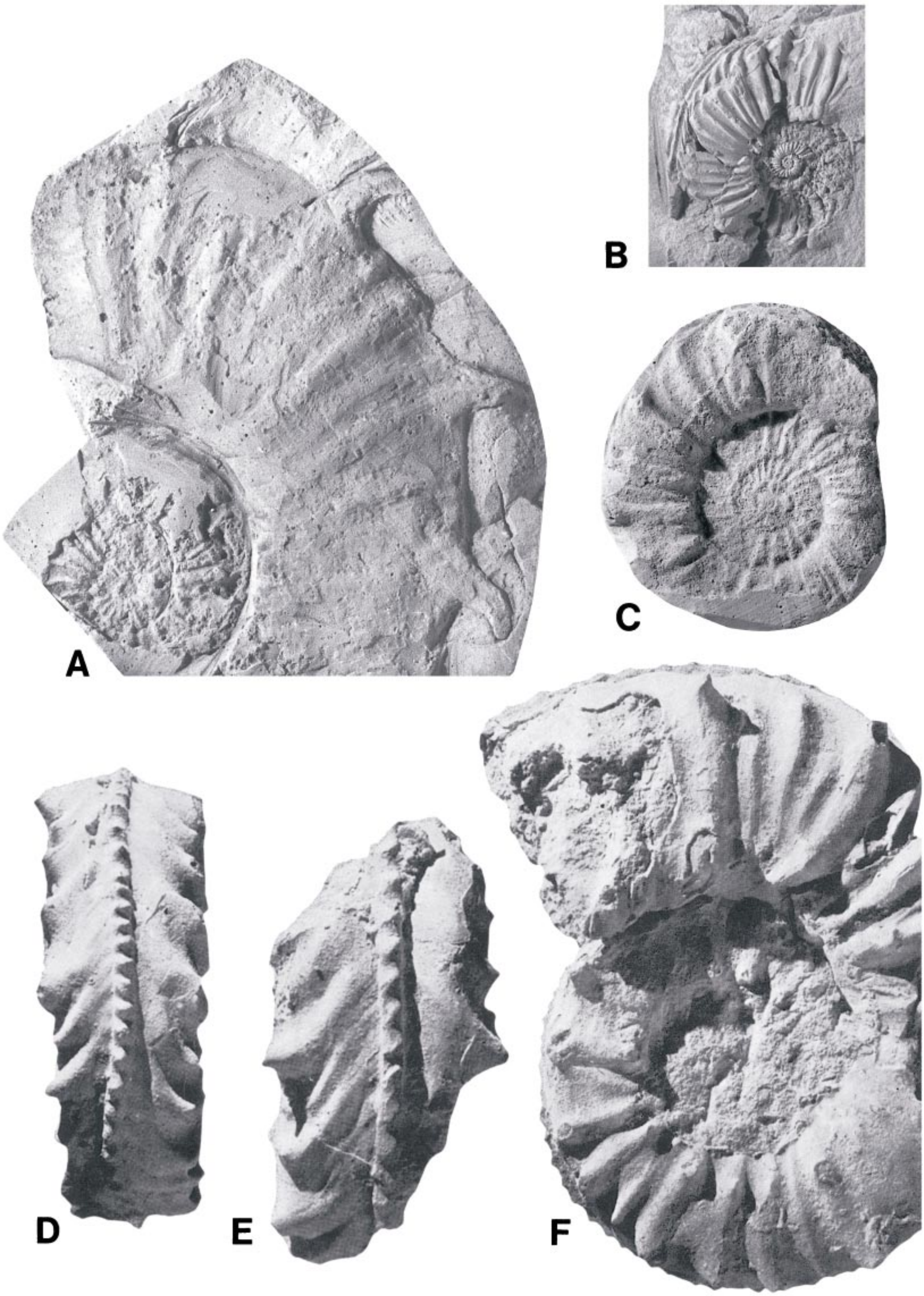


Fig. 107. Partial external suture of *Prionocyclus quadratus* Cobban, 1953. USNM 498451, from the Sage Breaks Member of the Carlile Shale in the SW¼ sec. 32, T. 50N, R. 66W, Crook County, Wyoming.

seam and bear well-developed umbilical bullae that migrate out to an inner flank position at as little as 20 mm diameter. These give rise to broad, blunt, crowded prorsiradiate ribs that are usually evenly developed, with only occasional irregularities. All bear feebly clavate to conical flat-topped inner ventrolateral tubercles that are the bases of long septate spines housed in grooves in the umbilical wall of the succeeding whorl, but rarely preserved (fig. 113X, Y). Low, broad, weakening ribs sweep forward and form an acute chevron with the line of the siphonal keel. Feeble outer ventrolateral clavi are present up to 15 mm diameter, but are thereafter lost, and the ribs are bituberculate. The strong siphonal keel is minutely and evenly crenulat-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ed. Larger specimens (figs. 113Q–S, V–Y, 114–118) vary in strength and coarseness of ribbing, with as few as 22 ribs of equal or unequal strength at 90 mm diameter, at which size the umbilical bullae migrate well out to the inner flank. This coarse, even or uneven ornament extends to the largest diameters seen.

The gracile form (figs. 109–112) has a whorl breadth to height ratio of 0.66–0.90 between 25 and 60 mm diameter (table 12). The coiling is evolute, with U = 35–40% of diameter; the umbilicus is shallow, with a low wall. Very crowded, even, primary ribs arise at the umbilical seam and strengthen across the flanks with no or only incipient bullae. Ribs are straight to feebly flexuous, and prorsiradiate on the flanks, where occasional long intercalated ribs yield a total of up to 70 ribs per whorl. Each rib bears a tiny conical to feebly clavate inner ventrolateral tubercle from which a weakening rib projects forward to form an acute ventral chevron with the minutely and evenly serrated siphonal ridge. Tiny outer ventrolateral clavi are present up to a diameter of approximately 10 mm, but are thereafter lost. From 60–150 mm this even style of ribbing continues, with around 36–40 ribs per whorl, which have feeble but variably developed umbilical bullae and inner ventrolateral clavi.

The suture is fairly simple, with a moderately deep lateral lobe (fig. 119).

DISCUSSION: Absence of an outer ventrolateral tubercle distinguishes this species from *Prionocyclus wyomingensis* when young, while the absence of an umbilical plus inner lateral tubercle separates it from *P. wyomingensis* when adult. The very even and sparser ribbing of *P. germani* alone serves to distinguish both juveniles and adults from *P. novimexicanus*. *Prionocyclus quadratus* generally has stouter quadrate whorls, and an incipient lateral tubercle when adult.

Ammonites schlönbachi Fritsch, 1872 (33, pl. 16, fig. 5) appears to be based on a poorly preserved crushed external mold of *P. germari*. A plaster cast taken from the mold, apparently the basis of the original figure, is shown as figure 108A. The flank ribs and long ventrolateral spines compare well with the Western Interior example shown in figure 113X, Y. Fritsch figured an undoubted juvenile *P. germari* from the same horizon and locality (1872: pl. 16, fig. 7).

Prionocyclus carvaholi Howarth, 1966 (p. 224, pl. 1, figs. 8–11; pl. 2, figs. 3–6; fig. 108D–F), from the Moçâmedes Desert, Angola, appears to be based on robust variants of the present species, even though Howarth (1966: 224) described very small ''upper or inner ventrolateral tubercles . . . represented merely by a raised portion of the rib obliquely in front of the ventrolateral spine.''

OCCURRENCE: Fairly abundant at the top of the Frontier Formation in central Wyoming (Cobban, 1990), and in the D-Cross Tongue of the Mancos Shale in south-central New Mexico. The species is also present in the basal part of the Austin Chalk in the Rio Grande area of southwestern Texas, where it was reported as *P. reesidei* (Freeman, 1961). In all of these areas, *P. germari* is associated with *Mytiloides incertus* (Jimbo) and *Eubostrychoceras matsumotoi* Cobban of late Turonian, *Scaphites corvensis/P. germari* Zone age. The species also occurs in the upper Turonian of Germany, the Czech Republic, and Angola.

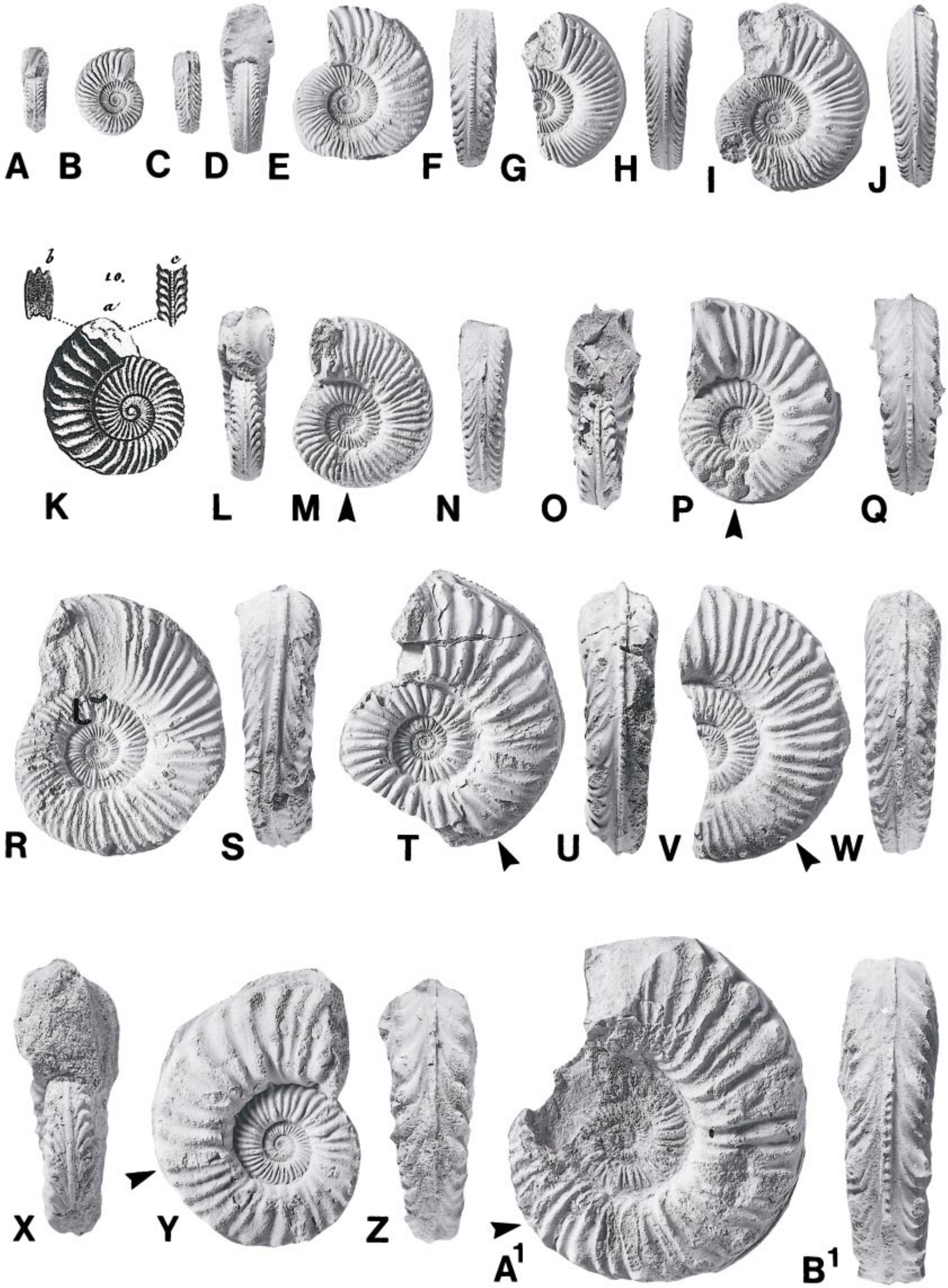
Prionocyclus pluricostatus, new species

Figure 120

DERIVATION OF NAME: *Plurimus* (Latin): most; *costatus* (Latin): ribbed.

←

Fig. 108. **A, B, D–F**. *Prionocyclus germari* (Reuss, 1845). **A**. plaster cast taken from the natural mold of the holotype of *Ammonites Schlönbachi* Fritsch, 1872: 33, plate 16, figure 5, from the upper Turonian *P. germari* Zone, Priesener Schichten near Werschowitz, Laun, Czech Republic. Narodni Museum, Prague, no. 004823. **B**. No. C16822 in the same collection, from the same unit near Cernovaly in the Czech Republic. **C**. The holotype of *Ammonites albinus* Fritsch, 1872: p. 28, plate 6, figure 4, from the Mallnitzer Schichten of Wehlowic, near Melnik, in the Czech Republic. **D–F**. The holotype of *Prionocyclus carvaholi* Howarth, 1966, from Ponta Grossa, 3.2 km SSE of Ponta des Salinas, 110 km N. of Moçâmedes, Angola. Copy of Howarth, 1966: plate 2, figures 3, 4, 6. All figures are ×1.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TYPES: Holotype is USNM 498491a (fig. 120D); paratypes USNM 498491b (fig. 120D), 498492 (fig. 120A), 498493 (fig. 120B), and 498494 (fig. 120C), all from USGS Mesozoic locality D11898, calcareous shale 4 m below the base of the Fort Hays Limestone Member of the Mancos Shale, upper Turonian, upper part of *Prionocyclus germari* Zone, NW¼, SE¼, sec. 22, T. 8 S, R. 87 W, Pitkin County, Colorado.

DIAGNOSIS: A densely and evenly ribbed *Prionocyclus*. There are up to 80 ribs per whorl in juveniles at 20 mm diameter, with inner ventrolateral clavi and outer ventrolateral clavi, if present, lost at a very early stage. Ribs may be single or arise in pairs or groups at the umbilical shoulder, or intercalate low on the flanks. Larger specimens with up to 90 ribs per whorl at 50 mm diameter, arranged as on nuclei, but bullate ribs bear strong inner ventrolateral clavi that are sometimes linked with weaker clavi or other ribs.

DISCUSSION: The types are crushed in shale, and there is little to add to the diagnosis. *Prionocyclus pluricostatus* n. sp. bears a superficial resemblance to *P. bosquensis* (fig. 76), also known only from crushed specimens in shales. They differ in that *P. bosquensis* has ribs of variable strength on nuclei, and persistent inner and outer ventrolateral tubercles. This last character separates the species from *P. wyomingensis* (see fig. 85A–C, F, G), whereas the eveness of ribbing separates it from *P. macombi* (fig. 67) and *P. novimexicanus* (fig. 88). *P. germari* (figs. 109, 113) has even ribbing, but specimens are never as densely ribbed as the present form. A specimen from New Mexico figured by Johnson (1903: 139, pl. 1, fig. 15) as *Prionocyclus* appears to be as densely ribbed as our species, but the New Mexico species is more involute.

The types occur with *Mytiloides incertus* at a very high level in the Turonian. We attribute them to the upper Turonian ammonite zone of *P. germari*, but they may represent a separate, as yet uncharacterized uppermost Turonian ammonite zone.

OCCURRENCE: As for types.

Genus *Prionocyclites* Kennedy, 1988

TYPE SPECIES: *Prionocyclites mite* Kennedy, 1988: 89, pl. 10, figs. 7–11; text-fig. 30.

DIAGNOSIS: ‘‘Inner whorls with distant bullate primary ribs separated by groups of weaker non-bullate primaries and occasional shorter intercalated ribs, all with a ventrolateral clavus. Keel broadly undulose, not serrated. Body chamber smooth but for distant bullate primaries and associated constrictions. Aperture constricted. Suture simple, with little-incised elements’’ (Kennedy, 1988: 89).

DISCUSSION: *Prionocyclites* is a progenetic dwarf, presumably derived from *Prionocyclus*, the inner whorls of the two sharing many common features (compare fig. 121 and fig. 51A–I), although the adult body chamber and simple adult suture of *Prionocyclites* are quite distinctive. It most closely resembles *Lymaniceras* Matsumoto, 1965, here interpreted as another progenetic dwarf collignoniceratid. However, *Lymaniceras* has a minutely serrated keel and lacks the *Prionocyclus*-like inner whorls and paucicostate, constricted body chamber of *Prionocyclites* (modified after Kennedy, 1988: 89).

OCCURRENCE: *Prionocyclus hyatti* Zone of north-east Texas only.

Prionocyclites mite Kennedy, 1988

Figures 121, 122

Prionocyclites mite Kennedy, 1988: 89, pl. 10, figs. 7–11, text-fig. 30.

Prionocyclites mite Kennedy. Emerson et al., 1994: 211, unnumbered figure on p. 213.

TYPE: Holotype by monotypy in USNM

←

Fig. 109. *Prionocyclus germari* (Reuss, 1845). **A–C**. USNM 498462; **D–F**. USNM 498463; **G, H**. USNM 498464; **I, J**. USNM 443834; all gracile forms from locality 26. **K**. copy of the original figure of the lectotype (Reuss, 1845: plate 7, figure 10), from the ‘‘Planermergel von Werschowitz.’’ **L–N**. USNM 498457; **O–Q**. USNM 498453; **R, S**. USNM 498458; **T, U**. USNM 220389; **V, W**. USNM 498459; **X–Z**. USNM 498465; **A¹**, **B¹**. USNM 498460, all gracile forms from locality 26. All figures are ×1.

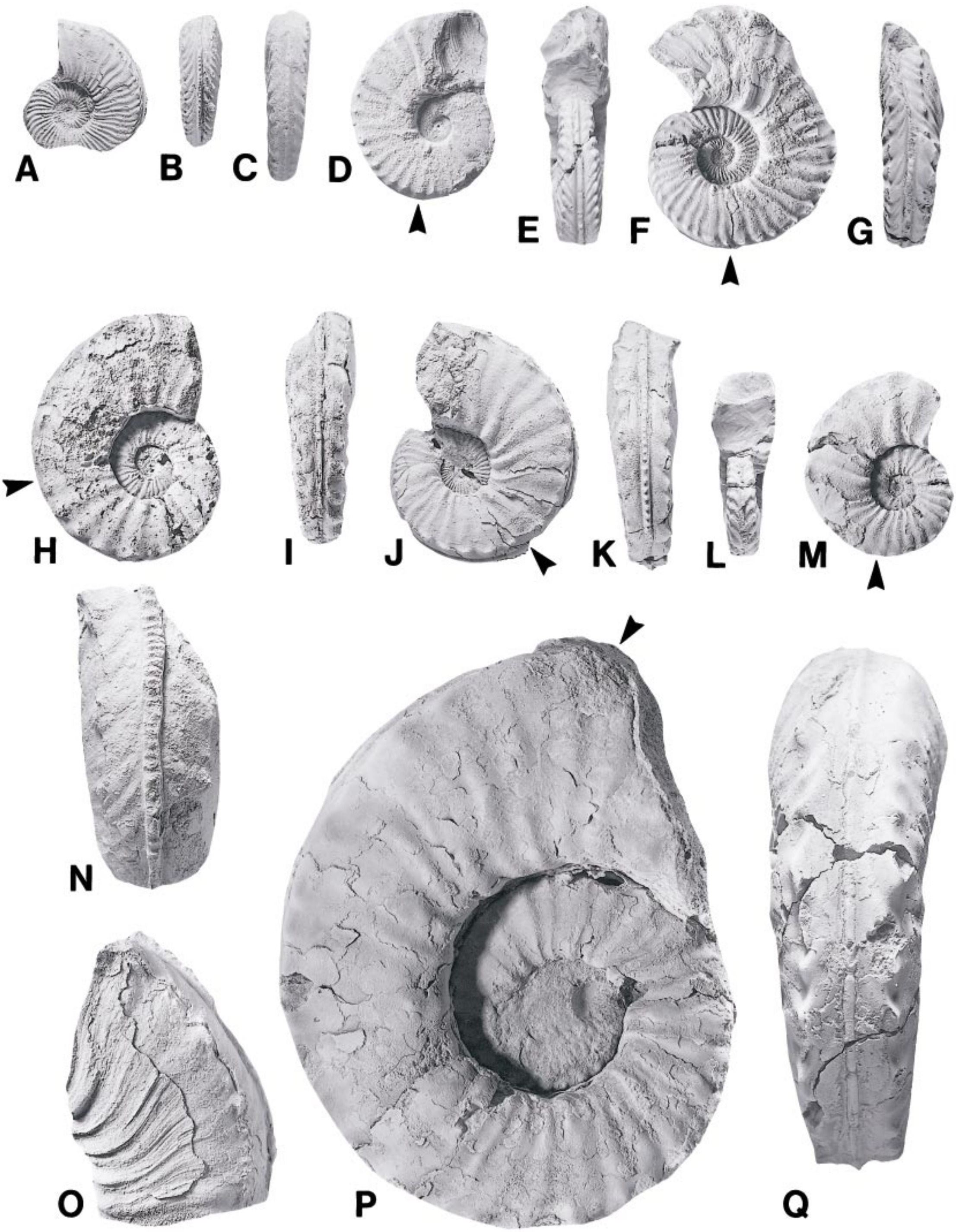

Fig. 110. *Prionocyclus germari* (Reuss, 1845). **A, B**. USNM 498466, gracile form from locality 59. **C, D**. USNM 498467, gracile form from locality 58. **E–G**. USNM 498468; **H, I**, USNM 498469; **J, K**. USNM 498470, all gracile forms from locality 59. **L, M**. USNM 498471, gracile form from locality 60. **N, O**. USNM 498472, gracile form from locality 61. **P, Q**. USNM 498473, from locality 58. All figures are ×1.

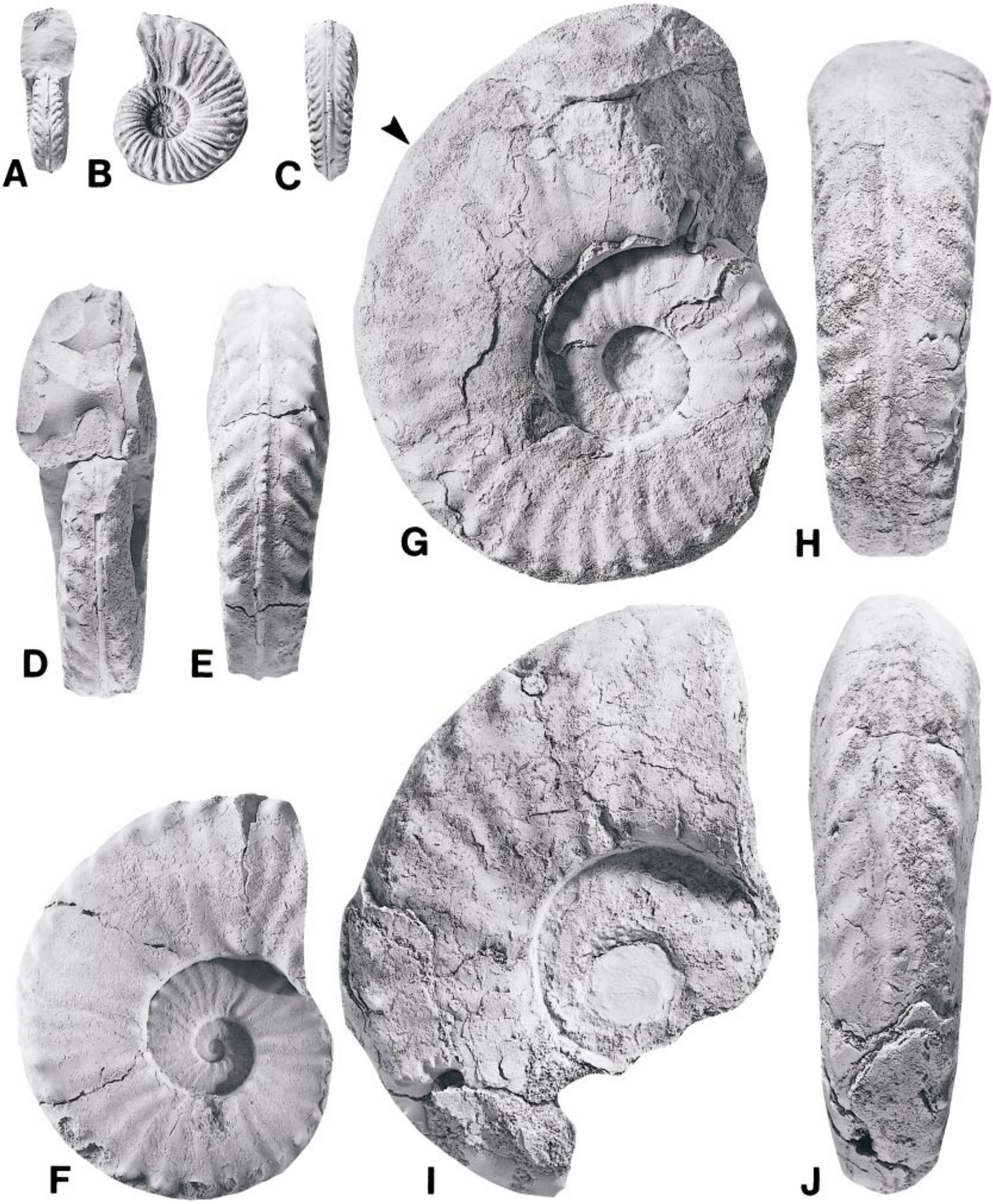

Fig. 111. *Prionocyclus germari* (Reuss, 1845). **A–C**. USNM 498474, gracile form from locality 58. **D–F**. USNM 498475, gracile form from locality 61. **G, H**. USNM 356922; **I, J**. USNM 498476, both gracile forms from locality 59. All figures are ×1.

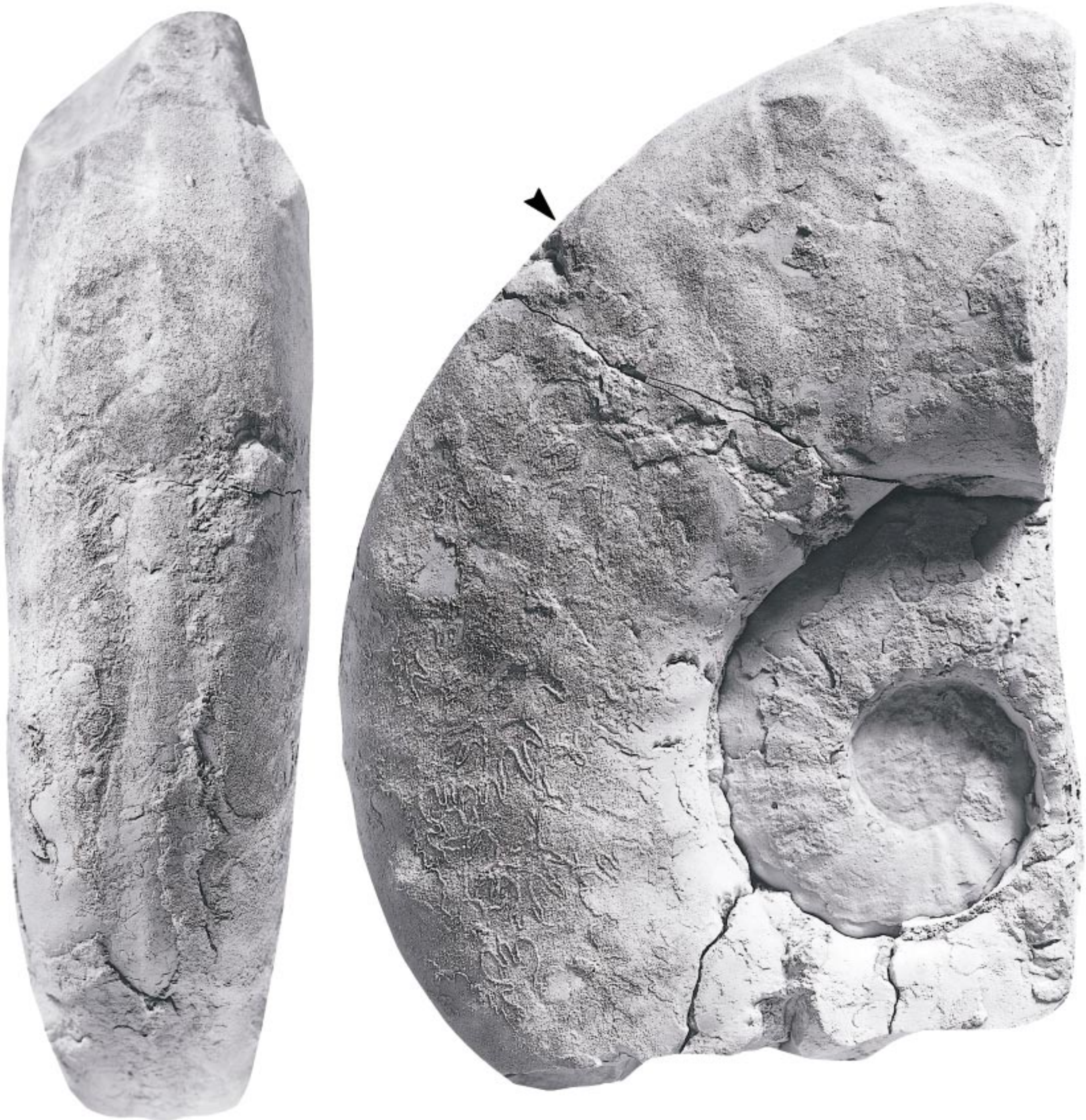

Fig. 112. *Prionocyclus germari* (Reuss, 1845). USNM 498477, a gracile form from locality 60. Figures are ×1.

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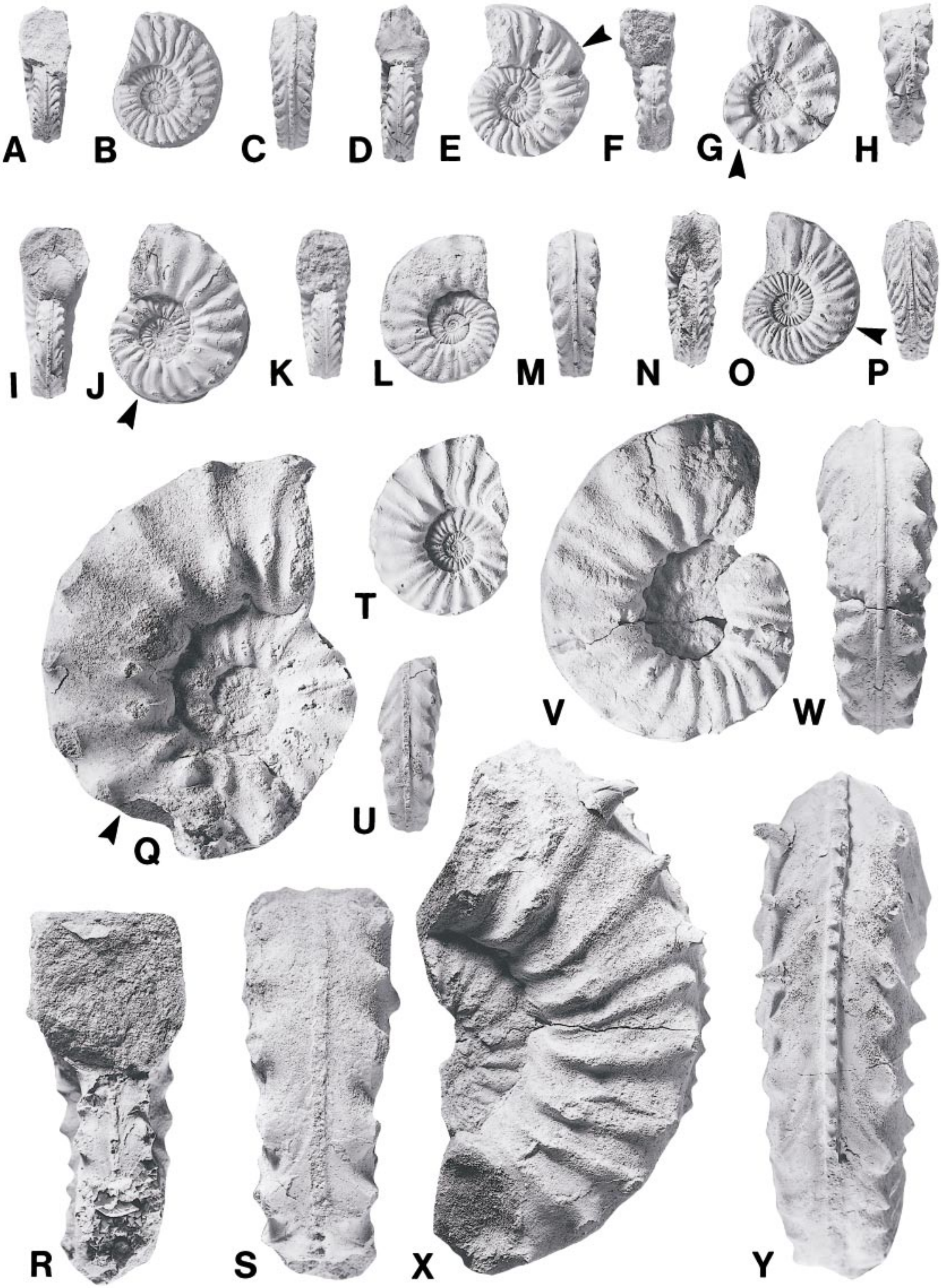
Fig. 113. *Prionocyclus germari* (Reuss, 1845). **A–C**. USNM 443832; **D, E**. USNM 498478; **F–H**, USNM 498452; **I, J**. USNM 498479; **K–M**. USNM 498480; **N–P**. USNM 498481; **Q–S**. USNM 498454; **T, U**. USNM 498482; **V, W**. USNM 498483; **X, Y**. USNM 443835, all robust forms from locality 26. All figures are ×1.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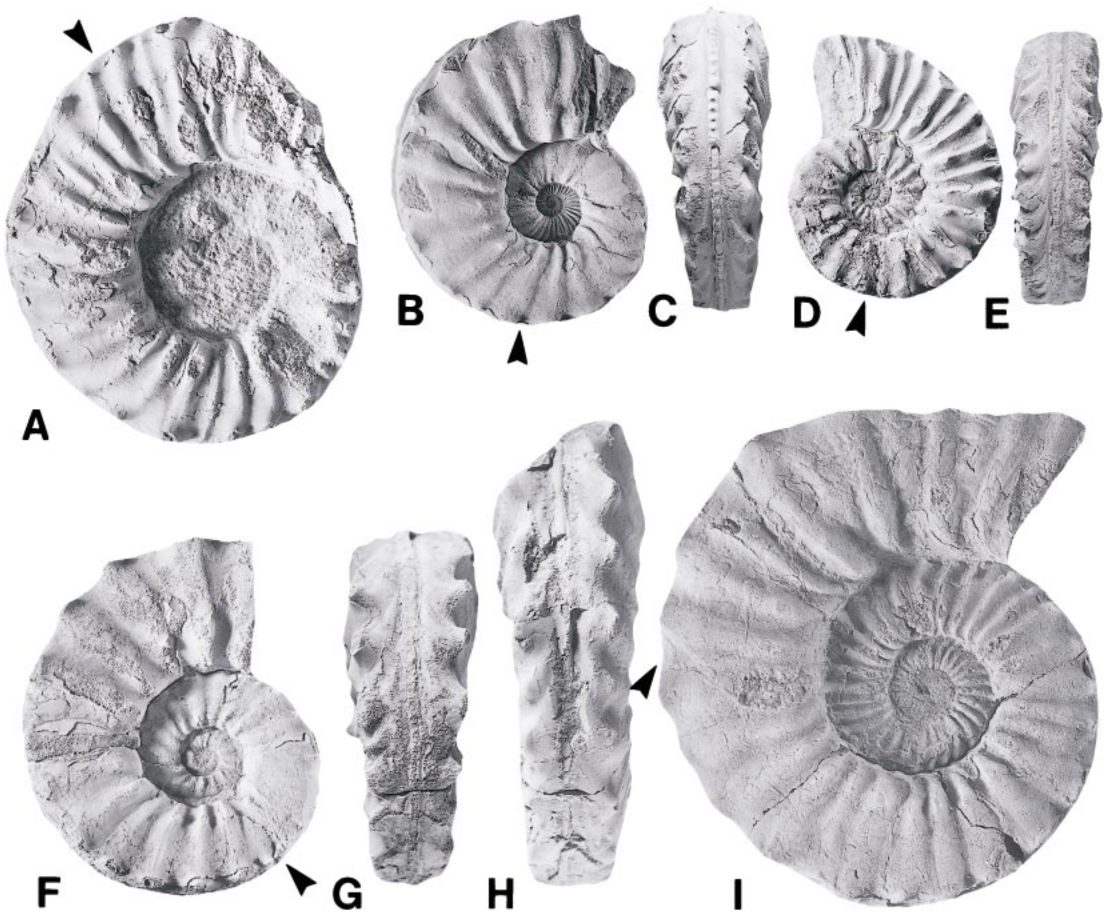

Fig. 114. *Prionocyclus germari* (Reuss, 1845). **A**. USNM 498484, robust form from locality 59. **B, C**. USNM 498485, robust form from locality 59. **D, E**. USNM 498486, robust form from locality 58. **F, G**. USNM 498487, robust form from locality 59. **H, I**. USNM 356920, robust form from locality 60. All figures are ×1.

420144 (figs. 121, 122; Table 13) from the Arcadia Park Formation, Eagle Ford Group at USGS locality 22608 (*ex* Renfro Collection), east of power plant on Mountain Creek Lake, Dallas County, Texas; *Prionocyclus hyatti* zone.

DIAGNOSIS: Small species characterized by its arched venter and prominent keel. Ribs are sparse, conspicuously prorsiradiate, and bear oblique ventrolateral clavi.

DESCRIPTION: ‘‘Holotype and only known specimen is a complete adult retaining traces of original shell. Coiling moderately evolute, with shallow umbilicus, umbilical wall low, rounded. Whorl section compressed with whorl breadth to height ratio 0.66. Flanks flattened, subparallel, with broadly round ventrolateral shoulders, venter with strong, blunt, undulose siphonal keel. On phragmocone there are twelve bullate ribs per whorl separated by two slightly weaker nonbullate ribs, giving a total of thirty-three to thirty-four ribs per whorl at the umbilical shoulder. Ribs are narrow, rounded, prorsiradiate, and straight on the inner flank, flexing forward and concave over the outer flank and ventrolateral shoulder. A few short ribs intercalate on the outer flank and all ribs bear a blunt, obliquely placed ventrolateral clavus. The ribs project forward from the clavus towards the mid-line of the venter but decline before reaching the keel. The low undulations on

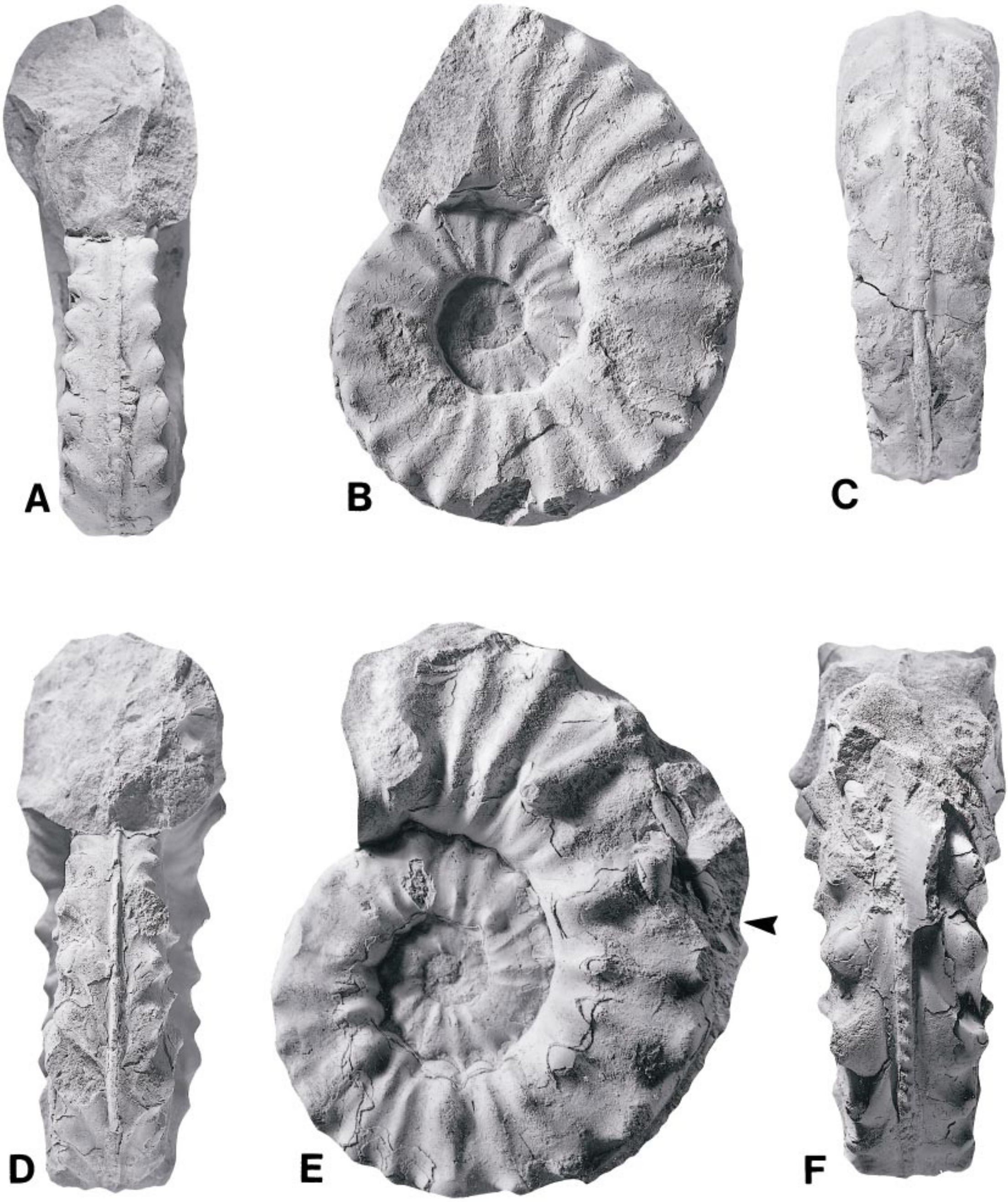

Fig. 115. *Prionocyclus germari* (Reuss, 1845). **A–C**, USNM 498488; **D–F**. USNM 498455, both robust forms from locality 59. All figures are ×1.

the keel do not correspond to the ribs; they are far fewer in number. This ornament extends on to the first part of the body chamber but thereafter rapidly declines. The last part of the body chamber is near-smooth between three very distant ribs that arise from prominent umbilical bullae. These ribs are narrow, rounded, and efface by the ventrolateral

Fig. 116. *Prionocyclus germari* (Reuss, 1845). USNM 498489, a robust form from locality 60. Figures are ×1.

Fig. 117. *Prionocyclus germari* (Reuss, 1845). USNM 498456, a robust form from locality 26. Figure is ×1.

shoulder. They are followed by a shallow constriction, most obvious at the ventrolateral shoulder. A much stronger constriction marks the adult aperture. Suture very simple with broad, little-incised E/L and narrower L; not approximated at the end of the phragmocone'' (Kennedy, 1988: 89).

DISCUSSION: The only ammonites with which *Prionocyclites mite* Kennedy, 1988, is likely to be confused are species of *Lyman-*

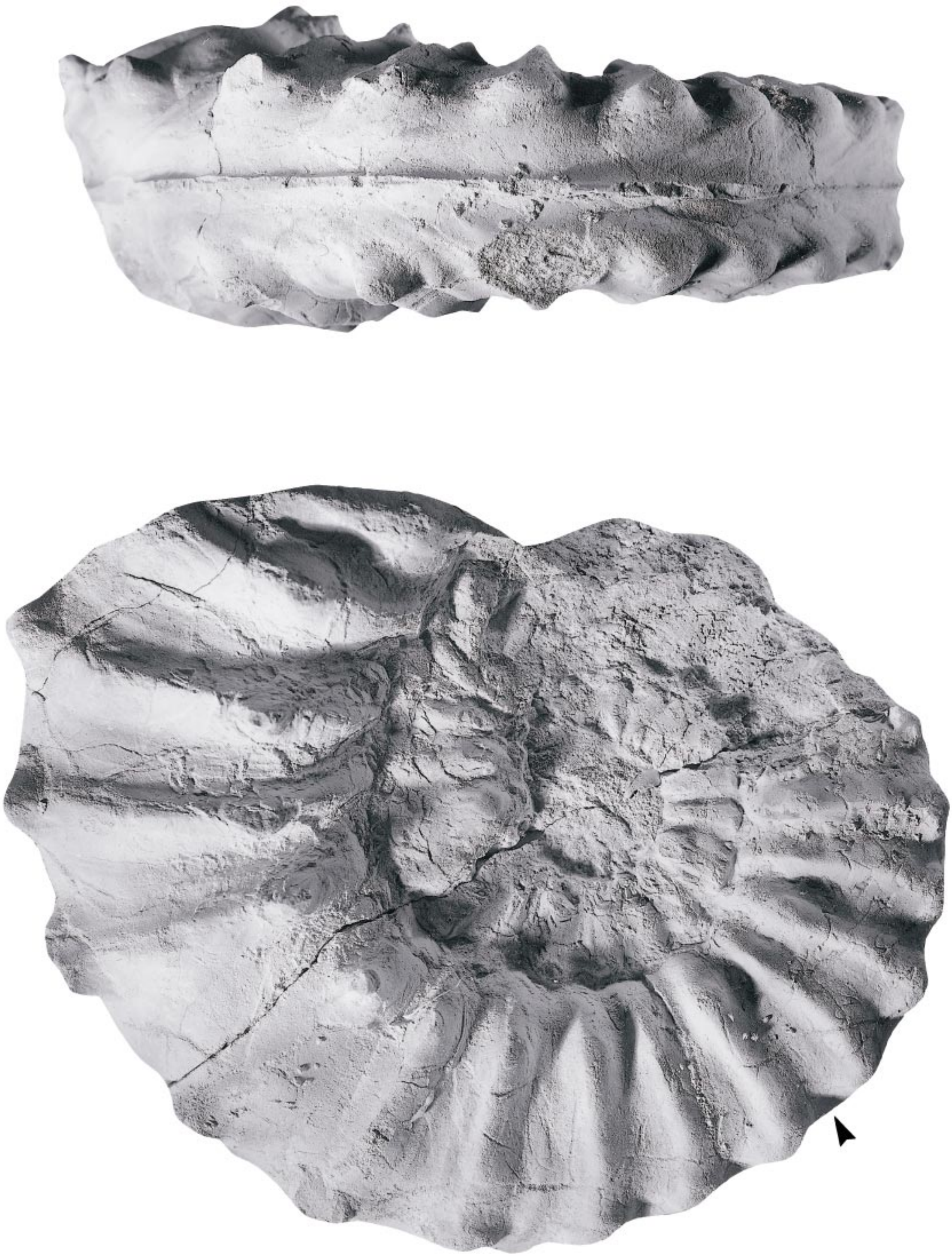

Fig. 118. *Prionocyclus germari* (Reuss, 1845). USNM 498490, a robust form from locality 57. Figure is ×1.

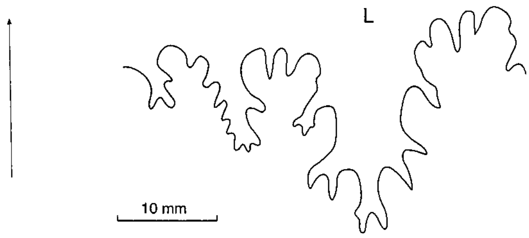

Fig. 119. *Prionocyclus germari* (Reuss, 1845). Partial external suture of USNM 498477 from the upper Turonian *P. germari* Zone D-Cross Tongue of the Mancos Shale at locality 60.

iceras Matsumoto, 1965. The type species, *L. planulatum* Matsumoto, 1965 (31, pl. 6, figs. 1, 2; pl. 7, figs. 1–5; pl. 8, figs. 1–8; text-figs. 10–16), is also a progenetic dwarf, but without the distinctive differentiation of primary ribs seen in *Prionocyclites* and with a finely serrated keel. Body chambers are very different.

OCCURRENCE: As for type.

Genus *Reesidites* Wright and Matsumoto, 1954

TYPE SPECIES: By original designation: *Barroisiceras minimum* (Yabe ms.) Hayasaka and Fukada, 1951: 325, pl. 1, figs. 1–4; pl. 2, figs. 1–7.

DIAGNOSIS AND DISCUSSION: See Matsumoto, 1965: 61.

OCCURRENCE: Upper Turonian, Japan, Tunisia, Armenia, Colombia, and New Mexico in the U.S. Western Interior.

Reesidites minimus (Hayasaka and Fukada, 1951)

Figures 123, 124

Barroisiceras minimum (Yabe ms.). Hayasaka and Fukada, 1951: 325, pl. 1, figs. 1–4; pl. 2, figs. 1–7.

Reesidites minimus Hayasaka and Fukada, 1951. Cobban and Kennedy, 1988: 66, figs. 1–3 (with full synonymy).

Reesidites minimum (Hayasaka and Fukada, 1951). Amédro, 1990: 270, pl. 25, figs. 4, 5 (with synonymy).

Reesidites minimus (Hayasaka and Fukada, 1951). Summesberger and Kennedy, 1996: 119, pl. 13, figs. 17, 19–23; text-figs. 15, 16.

TYPE: Holotype, by original designation, is the original of Hayasaka and Fukada, 1951: 326, pl. 4, figs. 1–4, from the Upper Turonian of the Ikushumbets, region Hokkaido, Japan.

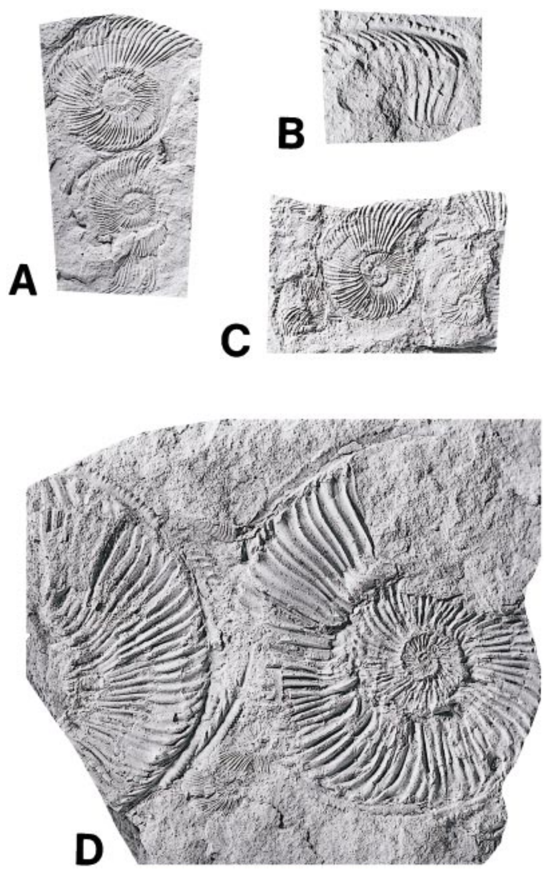

Fig. 120. *Prionocyclus pluricostatus* n. sp. **A**. Paratype USNM 498492; **B**. Paratype USNM 498493; **C**. Paratype USNM 498494; **D**. Holotype USNM 498491a (left), and paratype USNM 498491b (right), all from locality 34. All figures are ×1.

DIAGNOSIS: A compressed, involute species that attains a diameter of about 100 mm. The narrow cross section has flattened convergent and fastigiate venter with sharply defined ventrolateral shoulder. Ornament of low, broad, somewhat flexuous primary and secondary ribs, each supporting a low ventrolateral clavus and terminating in a midventral clavus. Primary ribs begin from low umbilical bullae.

DESCRIPTION: The smaller specimen, USNM 414511 (fig. 123A, B) is wholly septate. Coiling is very involute with an umbi-

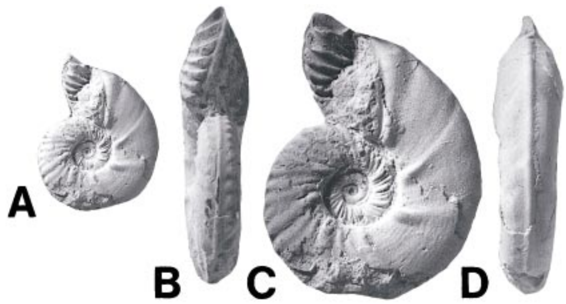

Fig. 121. *Prionocyclites mite* Kennedy, 1988. **A–D**. Holotype, USNM 420144, from locality 63. Figure **A** is ×1; Figures **B–D** are ×2.

licus to diameter ratio of 0.12; the umbilical wall is somewhat flattened. The whorl section is very compressed, with a whorl breadth to height ratio of 0.52, the greatest breadth at the umbilical bullae; the costal whorl section has flattened, convergent sides and a fastigiate venter. There are three distant umbilical bullae per half whorl. These give rise to pairs of low, broad, prorsiradiate ribs that are flexed back on the outer flanks. They strengthen across the flanks, and additional intercalaries arise low on the flanks to give a total of 13 ribs per half whorl. All ribs bear ventrolateral clavi and strong siphonal clavi on the crest of the fastigiate venter so that the shell has a strongly crenulate margin when viewed from the side.

The larger specimen, USNM 414510 (fig. 123C, D), is crushed, and preserves half a whorl of body chamber; it appears to be a nearly complete adult with the umbilical seam egressing markedly around the last half whorl. There are five umbilical bullae on the last half whorl of the phragmocone, corresponding to 18 ribs at the ventrolateral shoulder. The ribs arise in pairs from bullae. There are both long and short intercalaries and all are commonly flexed back and convex around midflank. All ribs terminate in ventrolateral clavi. The siphonal clavi are very prominent. On the body chamber the whorl section broadens somewhat and the venter rounds. The umbilical bullae decline and eventually disappear; most of the ribs are long, extending to the umbilical shoulder as both ribs and striae, while prominent growth lines develop. The ventrolateral and siphonal tubercles decline markedly towards the aperture.

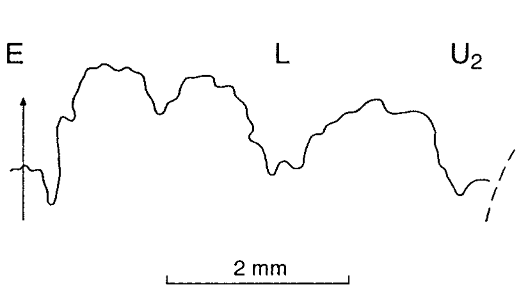

Fig. 122. External suture of *Prionocyclites mite* Kennedy, 1988. Holotype, USNM 420144, from locality 63.

The suture line has a markedly asymmetric, bifid E/L, the ventral half smaller than the dorsal; rectangular L that is deeper than E; asymmetrically bifid L/U_2; and relatively broad and bifid U_2 (fig. 124).

DISCUSSION: The larger, crushed specimen closely resembles the holotype, whereas the smaller matches that figured by Obata (1965: pl. 5, fig. 5). *Reesidites elegans* Matsumoto and Inoma, 1971 (in Matsumoto, 1971: 139, pl. 23, figs. 1–3; text-figs. 5–7) has much finer, more numerous, delicate, and weaker ribs than *R. minimus*. *R. latus* Matsumoto and Obata (1982: 82, pl. 6, fig. 2) is much more evolute, with U/D = 0.40 at maturity and a broader whorl. *R. subtuberculatus* (Gerhardt, 1897: 156, pl. 3, fig. 12) has much weaker flank ornament and tubercles.

OCCURRENCE: *Scaphites ferronensis*/*Prionocyclus wyomingensis* Zone of Valencia County, New Mexico and *Scaphites whitfieldi* Zone of Socorro County, New Mexico; upper Turonian of Japan, Austria, Tunisia, and Armenia.

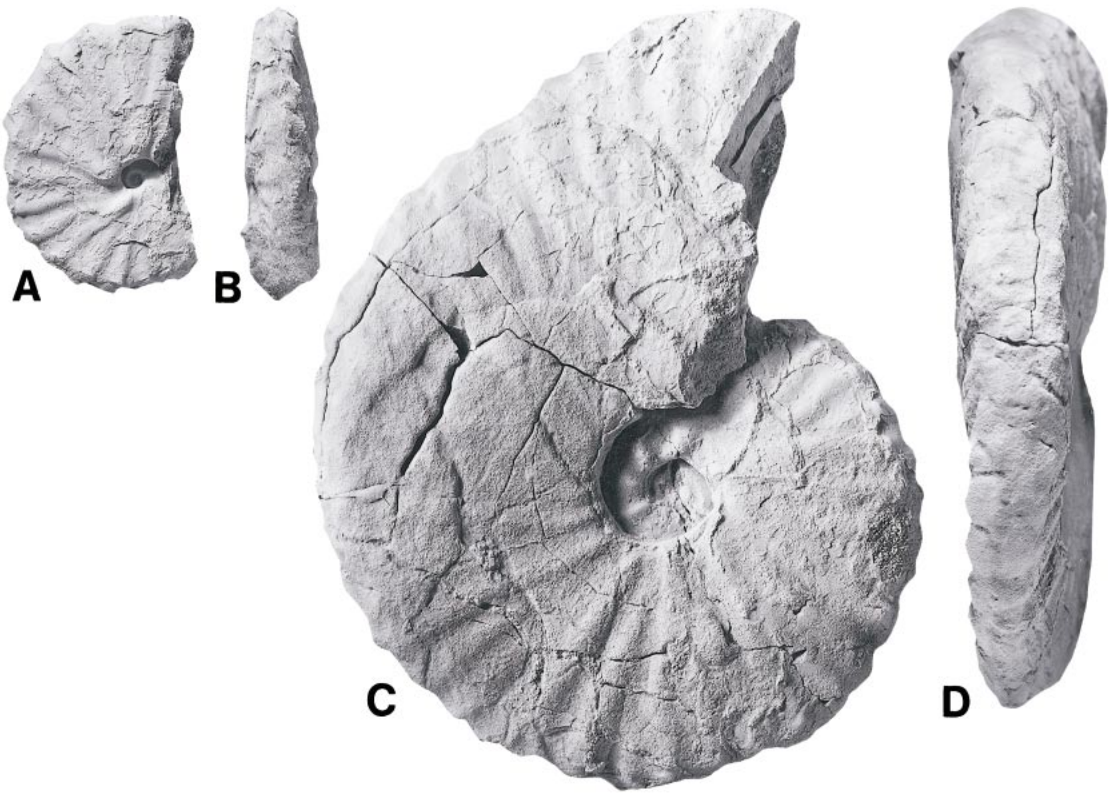

Fig. 123. *Reesidites minimus* (Hayasaka and Fukada, 1951). **A, B**. USNM 414511, from locality 43. **C, D**. USNM 414510, from locality 51. All figures are ×1.

ACKNOWLEDGMENTS

We thank R. E. Burkholder (who took most of the photographs) and the staffs of the Geological Collections in Oxford University Museum of Natural History and the Department of Earth Sciences, Oxford, and the Division of Paleontology (Invertebrates) at the American Museum of Natural History for technical assistance. J. M. Hancock (London/Shaftesbury), U. Kaplan (Gütersloh), R. Mapes (Ohio University, Athens), and P. Harries (University of South Florida, Tampa) critically reviewed an earlier version of the manuscript. Financial support of Kennedy by the Natural Environment Research Council, Royal Society, and Astor Fund (Oxford) is gratefully acknowledged. The U.S. Geological Survey kindly made the collections available for study.

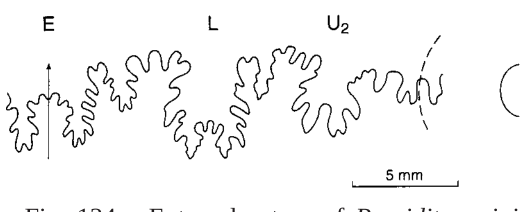

Fig. 124. External suture of *Reesidites minimus* (Hayasaka and Fukada, 1951). USNM 414511, from locality 43.

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