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Desmoinesian (Middle Pennsylvanian) orthocerid cephalopods from the Buckhorn Asphalt Lagerstätte in Oklahoma, Midcontinent North America

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Abstract. Nine longiconic cephalopod species of Desmoinesian (Middle Pennsylvanian; upper Carboniferous) pseudorthoceratid orthocerids are described from the Buckhorn Asphalt Lagerstätte (Boggy Formation) in Southcentral Oklahoma, Midcontinent North America. The fauna consists of *Pseudorthoceras knoxense* (McChesney), *Arbuckleoceras tricamerae* (Smith), *Bitaunioceras buckhornense* (Smith), *Cyrtothoracoceras*? sp., *Dolorthoceras boggyense* sp. nov., *Smithorthoceras unicamera* (Smith), *Sueroceras oklahomense* (Smith), *Sulphurnites taffi* sp. nov. and *Unklesbayoceras striatulum* sp. nov. *Bitaunioceras buckhornense* represents the first Pennsylvanian and therefore the oldest record of this genus. *Arbuckleoceras* gen. nov. differs from a comparable genus, *Shikhanoceras*, in possessing a weak exogastric curvature with a circular cross section of the conch and in lacking a conspicuous inflation at the embryonic shell. *Smithorthoceras* gen. nov. resembles orthoceratids rather than pseudorthoceratids in characters of camerae and siphuncle; however it refers to the Pseudorthoceratidae by having endosiphuncular deposits. These similarities seem to be the result of convergent evolution. Endosiphuncular deposits in *Sulphurnites* gen. nov. initiate at apical and adoral junctions between septal neck and connection ring, whose characters are unique for pseudorthoceratids. *Unklesbayoceras* gen. nov. differs from *Mitorthoceras* in having the endogastric conch, longer camerae and a less eccentric siphuncle. Taxonomic status of these orthoceratids was uncertain in previous biogeochemical and morphological studies. Sediments in the Buckhorn Asphalt Lagerstätte were deposited in a tropical epeiric sea (the Midcontinent Sea). Small, restricted marine basins, like that in this Oklahoma occurrence, probably provided an orthocerid refuge habitat as indicated by the high diversity and provincialism in comparison with other Middle Pennsylvanian (= Moscovian) faunas in other regions of the world.

Key words: Boggy Formation, Desmoinesian, Middle Pennsylvanian, Oklahoma, Orthocerida, Pseudorthoceratidae

Introduction

The Buckhorn Asphalt Quarry is situated approximately 10 km south of the community of Sulphur in Murray County, Southcentral Oklahoma, Midcontinent North America (Figure 1). Deposits in the quarry contain one of the best preserved Palaeozoic faunas in the world. Because of the outstanding preservation with impregnated hydrocarbons, Seuss *et al*. (2009) termed the locality as an "Impregnation Fossil Lagerstätte". This study documents the orthocerid cephalopod fauna from this Lagerstätte.

The Buckhorn Asphalt Lagerstätte belongs to the Boggy Formation, the name that was introduced by Taff (1899) for a Middle Pennsylvanian (upper Carboniferous) marine unit in south-central to south-eastern Oklahoma. Shale is predominant in the formation with subordinate amounts of sandstone, coal, and limestone (Ham, 1969; Hemish and Suneson, 1997). The top of the formation has been removed by erosion in the Buckhorn Asphalt Quarry, where the Virgilian (Upper Pennsylvanian) Ada Formation unconformably overlies the older unit (Squires, 1973). Asphalt stained deposits are found below the unconformity only and have a thickness of approximately 10 m. The specimens examined in this study were collected from the asphaltic limestone

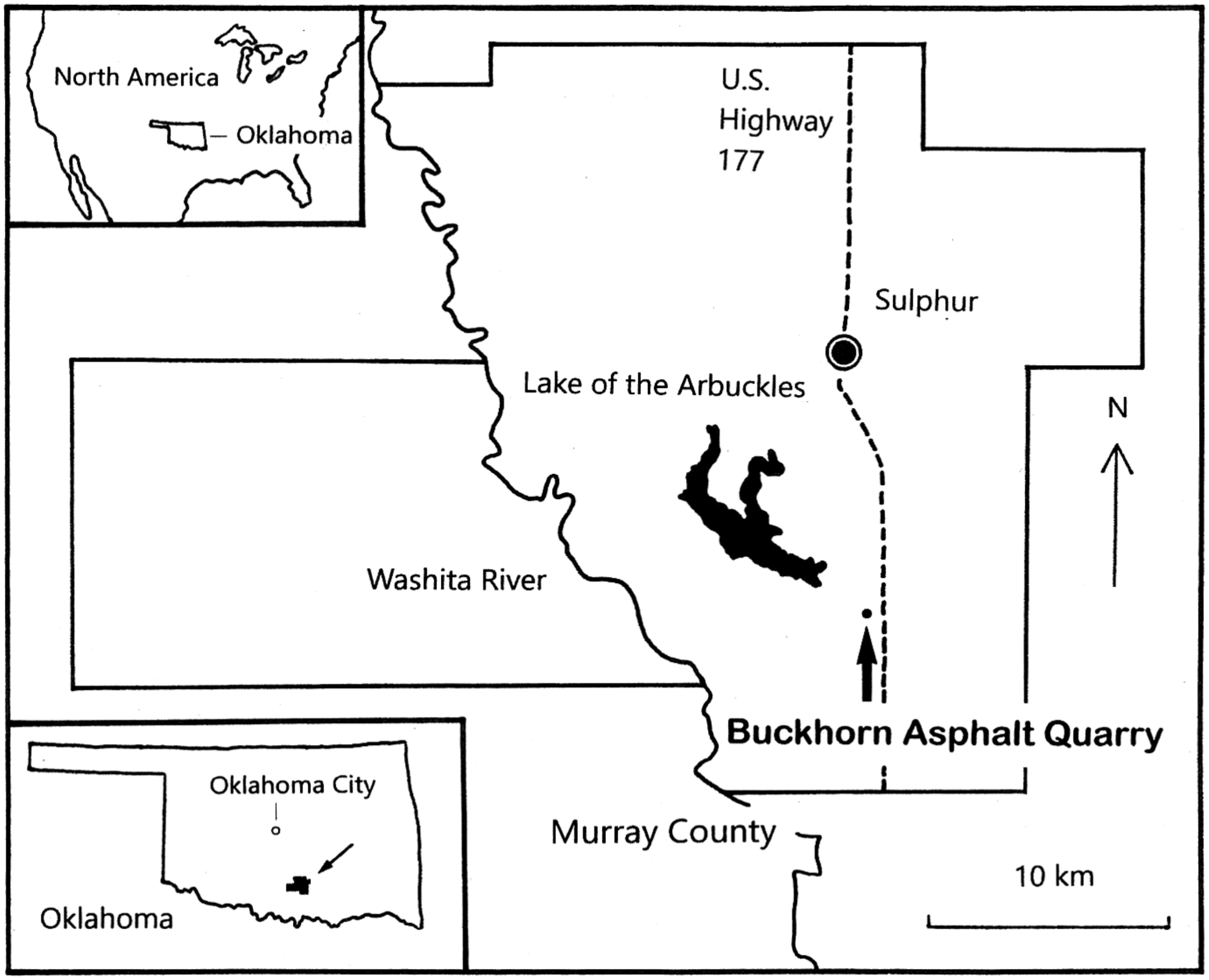

Figure 1. Map showing the geographic position of the Buckhorn Asphalt Lagerstätte (= locality OKD-53; GPS NAD84: 34°26′44″N, 96°57′41″W) in Murray County, Southcentral Oklahoma, North America.

("cephalopod coquina"; see Figure 2) that is 0.5 m thick and 3.5 m below the unconformably upper surface of the deposits (Seuss *et al*., 2009; Ernst *et al*., 2016). Rowland *et al*. (1973) recorded the fusulinids *Fusulina* and *Wedekindellina* from the cephalopod horizon that indicate Desmoinesian (= Moscovian; upper Carboniferous) age, and this age assignment is supported by the ammonoid fauna summarized by Unklesbay (1962).

Repositories.—The specimens examined are reposited in the American Museum of Natural History in New York City (prefixed AMNH) and in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (prefixed BSPG).

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Pseudorthoceratoidea Flower and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Pseudorthoceratinae Flower and Caster, 1935

Genus ***Pseudorthoceras*** Girty, 1911

Type species.—*Orthoceras knoxensis* McChesney, 1859.

Pseudorthoceras knoxense (McChesney, 1859)

Figure 3A–C, G

Orthoceras knoxensis [*sic*] McChesney, 1859, p. 69.
Pseudorthoceras knoxense (McChesney). Girty, 1911, p. 143; Sturgeon *et al*., 1997, p. 23, pl. 1–3, figs. 1–21 [with earlier synonymy];

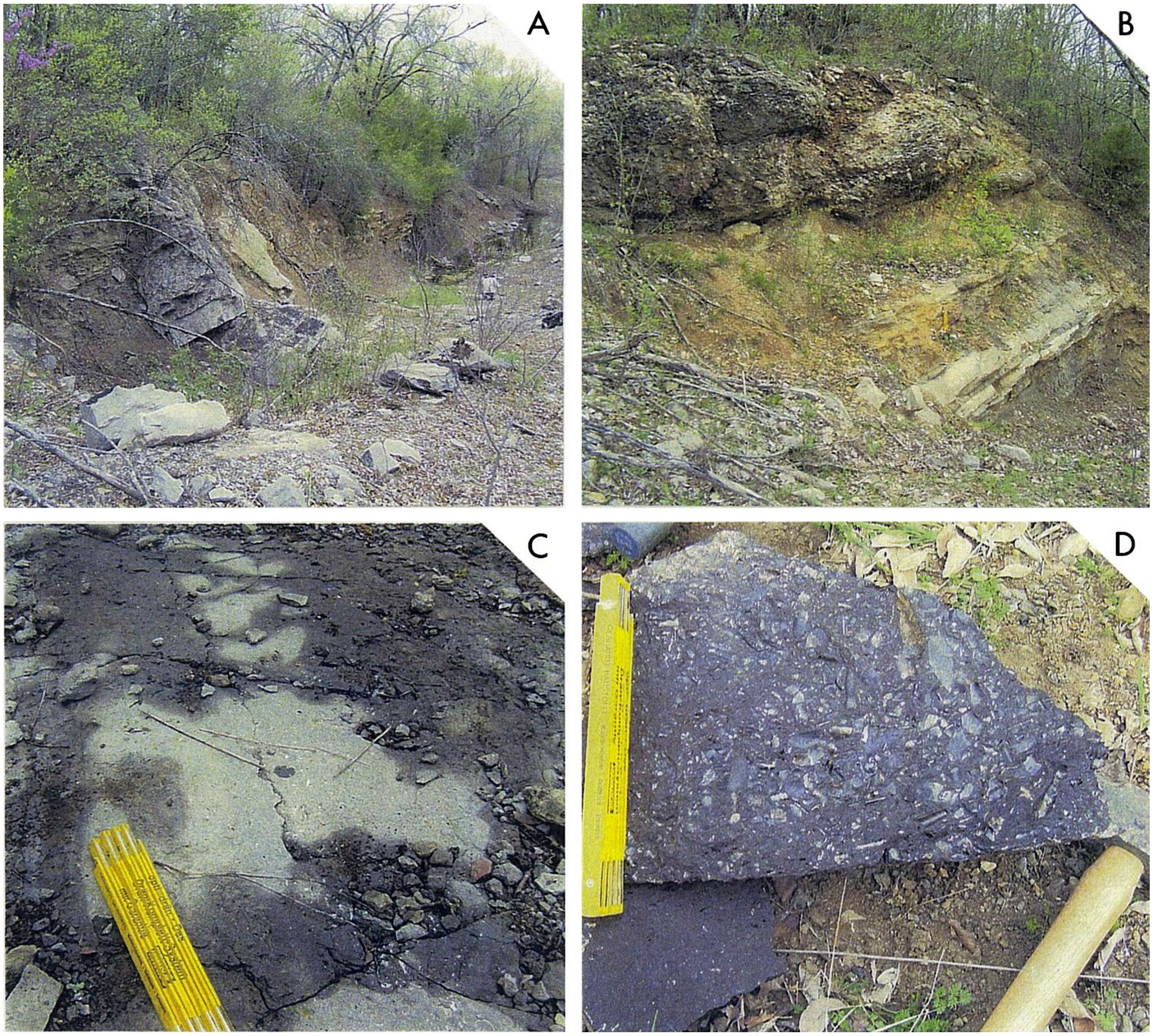

Figure 2. The Buckhorn Asphalt Lagerstätte. **A,** a full view into the northeastern area of the Buckhorn Asphalt Quarry. **B,** an outcrop showing unconformity between the Ada and Boggy Formations. Asphalt-stained deposits are found just below this unconformity. **C,** the floor of the quarry that is mainly built by the "cephalopod coquina". **D,** freshly broken block of the "cephalopod coquina" showing the intense stain with asphalt and the high amount of cephalopod fragments.

Kröger and Mapes, 2004, p. 562, figs. 1.7, 4, 5.9, 6.7, 6.15 [with additional synonymy].

Description.—Two fragmentary specimens including an apical shell and a deformed more adoral phragmocone are available for this study; they are longiconic orthocones; embryonic shell exhibits faint endogastric curvature; except for vicinity of apex that has very weak longitudinal lirae, shell surface lacks ornamentation. Sutures directly transverse; camerae short; dorsoventral section prepared from adoral shell shows siphuncular structure of cyrtochoanitic septal necks and strongly inflated ventral connecting rings; dorsal part of the larger specimen is mostly crushed. Endosiphuncular deposits form continuous lining on ventral siphuncular wall; cameral deposits differentiated into episeptal-mural and hyposeptal.

Material examined.—AMNH 5892, 5893.

Discussion.—Numerous specimens exhibiting wide morphological variations have been assigned to *Pseudorthoceras knoxense*, whose stratigraphic range is exceptionally long, with a range spanning the Chesterian (Late Mississippian, early Carboniferous; Kröger and Mapes, 2004) to Wordian (middle Permian; Gordon, 1964).

Figure 3. **A–C, G,** *Pseudorthoceras knoxense* (McChesney, 1859); A, G, AMNH 5893; A, ventral view; G, dorsoventral thin section, showing ventral siphuncular wall; B, C, apical shell, AMNH 5892; B, ventral view; C, lateral view, venter on right. **D,** *Dolorthoceras boggyense* sp. nov., paratype, AMNH 5917, dorsoventral thin section, venter on left. **E, F, H–J,** *Sulphurnites taffi* sp. nov., holotype, AMNH 5997; E, lateral view, venter on right; F, septal view, venter down; H, dorsoventral thin section, venter on left; I, partial enlargement of H to show dorsal septal neck; J, partial enlargement of H to show details of siphuncular structure. Arrows in J indicate incipient parts of endosiphuncular deposits. **K,** *Smithorthoceras unicamera* (Smith, 1938), AMNH 5959, dorsoventral thin section, venter on right, showing details of cameral and endosiphuncular deposits (arrow). Scale bar is 40 mm in A; 20 mm in B, C, E; 8 mm in D, G, H; 10 mm in F; 0.8 mm in I; 3.3 mm in J; 4 mm in K.

Pseudorthoceras knoxense was first recorded by Smith (1938, p. 5, 6, pl. 1, figs. 10–12) from the Buckhorn Asphalt Lagerstätte. Characters of the present specimens also fall within the morphologic range of *P. knoxense* accepted by previous workers. However, direct comparison between them and the syntypes from the Pennsylvanian McLeansboro Group of Illinois is difficult, because the original description by McChesney (1859) is too simple to clarify their details and his publication lacks illustrations. There is a possibility that this taxon contains several not yet described species or subspecies. This would require reexamination of the types and revision of the specific diagnosis.

Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus ***Arbuckleoceras*** gen. nov.

Type species.—*Orthoceras tricamerae* Smith, 1938, by monotypy.

Diagnosis.—Conchs longiconic with weak exogastric curvature, gradual expansion and circular cross sections; shell surface except apical portion lacks ornamentation; apex bluntly pointed, marked by transverse and longitudinal surface lirae; sutures directly transverse; camerae relatively long; siphuncle nearly central in position; septal necks short and orthochoanitic to suborthochoanitic; connecting rings cylindrical; parietal endosiphuncular and mural cameral deposits recognized.

Etymology.—The generic name is derived from the Arbuckle Mountains, and the locality of the type species of the new genus is situated at the northern edge of these mountains.

Discussion.—Possession of the cylindrical connecting rings and the parietal endosiphuncular deposits warrant a subfamilial assignment of *Arbuckleoceras* gen. nov. In known genera of Spyroceratinae, *Arbuckleoceras* is most similar to the early Permian genus, *Shikhanoceras* Shimansky, 1954, from the southern Urals. However, a conspicuous inflation at the embryonic shell, which represents the most characteristic diagnostic feature of *Shikhanoceras*, is not developed in *Arbuckleoceras*. Differences in the shapes of the adoral conch, i.e., *Arbuckleoceras* shows a weak exogastric curvature with circular cross section, whereas *Shikhanoceras* has orthoconic and laterally compressed conchs. These features are useful to distinguish between these genera.

Dolorthoceras Miller, 1931, is a well known and widespread genus ranging from the Early Devonian to early Permian (Flower, 1939; Sweet, 1964). This genus also resembles *Arbuckleoceras*, but it differs in having an orthoconic conch and subcylindrical to barrel-shaped connecting rings with an abrupt constriction at the septal foramina. In addition, the camerae of *Dolorthoceras* are shorter than those of *Arbuckleoceras*.

Arbuckleoceras tricamerae (Smith, 1938)

Figures 4, 6N

Orthoceras tricamerae Smith, 1938, p. 9, pl. 1, figs. 8, 9.
"*Orthoceras*" sp. A, Ristedt, 1971, pl. 28, fig. 19, pl. 29, fig. 1, pl. 31, fig. 2, pl. 34, fig. 6, pl. 36, figs. 1, 3, 4, pl. 37, figs. 1, 4, 5, pl. 38, figs. 1, 2, 6, 7, 9, pl. 39, figs. 1, 2, 4–6, 9, pl. 42, figs. 2, 6; Tanabe and Uchiyama, 1997, fig. 9.
Orthoceras sp., Blind, 1987, pl. 1, figs. 5, 6, pl. 3, fig. 2, pl. 4, figs. 1–4; text-figs. 2, 5, 7; 1988, text-figs. 1, 5, 7D, 9B, 10A–F; 1991, pl. 1, figs. 1–6, pl. 2, figs. 1–5, pl. 3, figs. 1–6, pl. 4, figs. 1–6, pl. 5, figs. 1–6, pl. 6, figs. 1–6.
Orthoconic nautiloid, Sadd, 1991, figs. 8-A, B; Seuss *et al*., 2012a, fig. 3C.
Pseudorthoceras sp., Seuss *et al*., 2009, fig. 17I.

Description.—Longiconic conchs with weak exogastric curvature and circular cross sections; conch expansion is gradual, 4–5° in angle; except for apical portion, shell surface lacks ornamentation; no peristome preserved. Embryonic shell indicates asymmetrical profile in lateral view; apex shifts to ventral side and is bluntly pointed; apical angle approximately 40° in lateral view; the most apical portion of 1.3 mm length from apex has transverse lirae; in addition, weak longitudinal lirae forming cancellate ornamentation are developed on ventral surface of this portion. Sutures directly transverse; camerae relatively long for the family, indicating form ratios (maximum width/length) of 1.5–1.9; siphuncle nearly central in position; siphuncular wall consists of orthochoanitic to suborthochoanitic septal necks and thin connecting rings; length of septal necks short, 0.27–0.29 mm at approximate conch diameter of 4 mm; shapes of connecting rings are cylindrical with very weak constrictions at septal foramina. Endosiphuncular deposits are weak; thin parietal deposits developed on ventral siphuncular wall; cameral deposits mural.

Material examined.—AMNH 5894–5913.

Discussion.—Morphologies of the examined specimens herein agree well with the specific definition of *Orthoceras tricamerae* Smith, 1938, described from the Buckhorn Asphalt Quarry. The diagnosis of *Orthoceras* Bruguière, 1789, was emended by Flower (1962) as a genus having three longitudinal furrows at mid-length of the body chamber and the empty siphuncle. Thus, the generic placement by Smith (1938) is revised.

Well preserved embryonic shells of *Arbuckleoceras tricamerae* were documented by Ristedt (1971) and Tanabe and Uchiyama (1997) as "*Orthoceras*" sp. A and by Blind (1987, 1988, 1991) as *Orthoceras* sp. Their results reveal the presence of a distinct cicatrix that is not observed in the present material owing to sediment coverage.

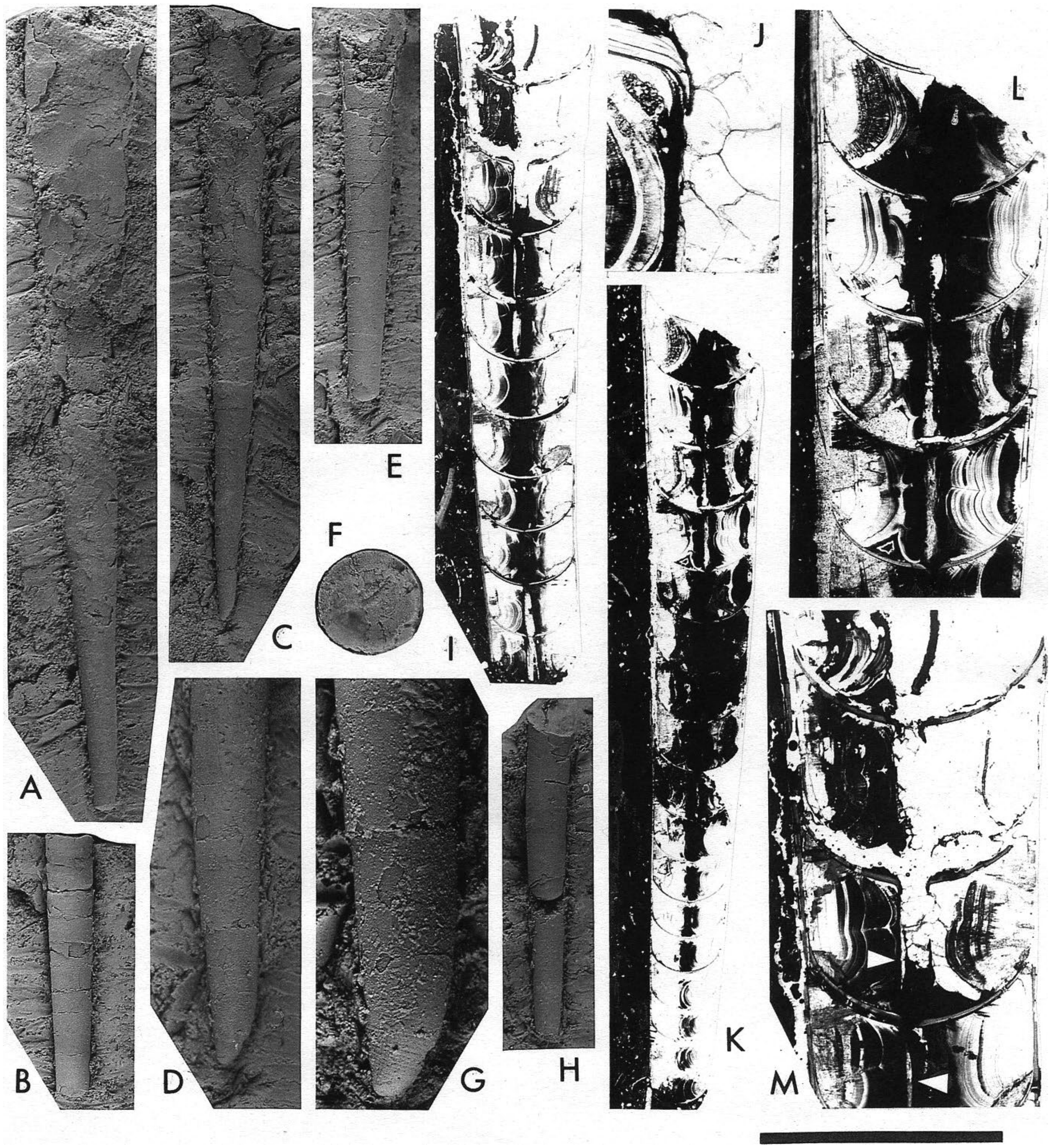

Figure 4. *Arbuckleoceras tricamerae* (Smith, 1938). **A,** AMNH 5896, lateral view, venter on left; **B, F, I, J, M,** AMNH 5990; B, dorsal view; F, septal view of adoral end, venter down; I, dorsoventral thin section, venter on left; J, partial enlargement of I, showing details of details of ventral septal neck; M, partial enlargement of I to show details of cameral and endosiphuncular deposits (arrows); **C, D, G,** AMNH 5903; C, lateral view, venter on left; D, G, partial enlargements of C, showing details of apical shell; **E,** AMNH 5897, ventral view; **H, K, L,** AMNH 5898; H, ventral view; K, dorsoventral thin section, venter on right; L, partial enlargement of K to show details of cameral deposits. Scale bar is 20 mm in A–C, E, H; 8 mm in D, I, K; 10 mm in F; 4 mm in G, L, M; 0.8 mm in J.

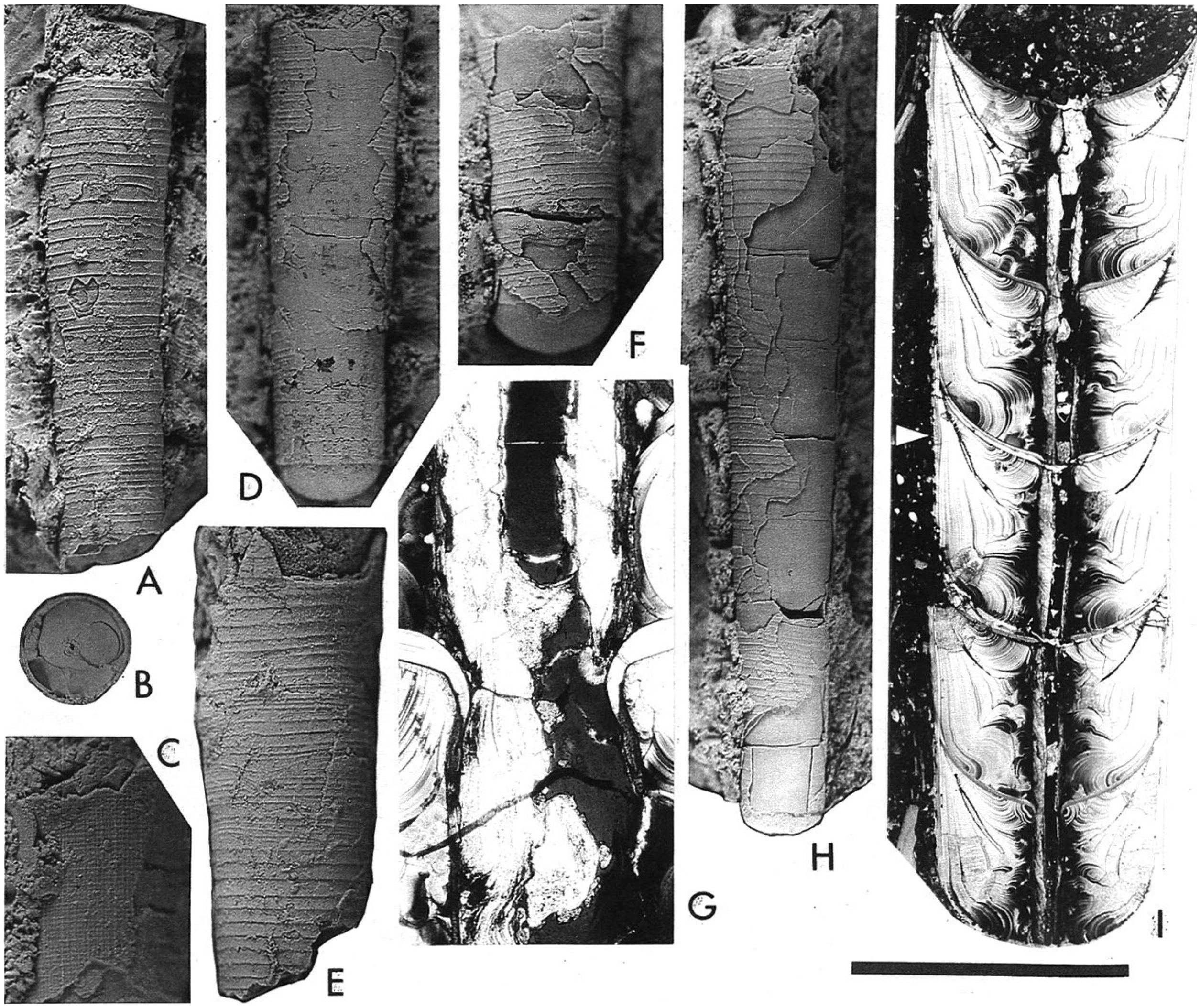

Figure 5. **A, B, D–I,** *Bitaunioceras buckhornense* (Smith, 1938). A, B, AMNH 5981; A, dorsal view; B, septal view of apical end, venter down; D, G, I, AMNH 5979; D, dorsal view; G, partial enlargement of I to show details of siphuncle; I, dorsoventral thin section, venter on left; E, AMNH 5985, side view; F, AMNH 5978, lateral view, venter on left; H, AMNH 5980, lateral view, venter on right. Arrow in I indicates shell constriction. **C,** *Sueroceras oklahomense* (Smith, 1938), AMNH 5996, details of surface ornamentation. Scale bar is 8 mm in A, B, D–F, H; 4 mm in C, I; 0.8 mm in G.

Genus ***Bitaunioceras*** Shimizu and Obata, 1936

Type species.—*Orthoceras bitauniense* Haniel, 1915.

Discussion.—See Niko and Nishida (1987) for discussions, including diagnostic emendations, superfamilial to subfamilial assignments and constituent species, of the genus *Bitaunioceras*.

Bitaunioceras buckhornense (Smith, 1938)

Figure 5A, B, D–I

Orthoceras indianum var. *buckhornense* Smith, 1938, p. 9, pl. 1, fig. 7.

"*Orthoceras*" with imbricate ornamentation, Fisher and Teichert, 1969, p. 11, text-fig. 6.

Dolorthoceras incisum Gordon, 1964. Crick, 1982, pl. 1, figs. 1, 4.

Dolorthoceras caneyanum (Girty, 1909). Crick, 1982, pl. 1, fig. 5.

Description.—Longiconic orthocones with circular cross sections and gradual conch expansion, 3–4° in angle; shell surface is ornamented by distant transverse lirae; there are 2–6 lirae per 1 mm at approximate conch diameter of 4 mm; internal mold of conch marked by shallow transverse constrictions due to internal thickening of shell walls; distance of adjoining constrictions nearly equals corresponding conch diameter; peristome and embryonic shell are unknown. Sutures directly transverse; camerae long with maximum width/length ratios of 1.3–1.5; septal curvature deep; siphuncle central in position; siphuncular wall consists of suborthochoanitic septal necks and thin connecting rings; length of septal necks is short, 0.21–0.29 mm at conch diameter of approximately 4 mm; shapes of connecting rings are subcylindrical with weak constrictions at septal foramina. Thick parietal endosiphuncular deposits developed on ventral and dorsal siphuncular walls; ventral deposits form continuous lining; cameral deposits well developed, episeptal-mural and hyposeptal.

Material examined.—AMNH 5977–5991.

Discussion.—The present cephalopod taxon was proposed by Smith (1938) as a variety of *Orthoceras indianum* Girty (1909, p. 47, pl. 6, figs. 13, 13a) from the Chesterian (Upper Mississippian; = lower Carboniferous) Caney Shale in Oklahoma on the basis of similarities of gross conch shape and surface ornamentation. However, a phylogenetic relationship between these two taxa is uncertain because of the unknown internal morphologies of the Mississippian species.

The transverse constrictions made by internal shell wall thickenings of this species warrant a placement in *Bitaunioceras*. The discovery from the Desmoinesian rocks represents the oldest and first Pennsylvanian record of this genus. Previous stratigraphic records of the genus range from the Sakmarian (lower Permian) of the southern Urals (Shimansky, 1954) and central Japan (Niko and Nishida, 1987) to the Guadalupian (middle Permian) of Sicily (Gemmellaro, 1890) and northern Mexico (Miller, 1944).

Genus ***Cyrtothoracoceras*** Turner, 1954

Type species.—*Cyrtoceras tuberculatum* M'Coy, 1844.

Cyrtothoracoceras? sp.

Figure 6A, B

? *Thoracoceras* sp., Seuss *et al*., 2009, fig. 17K.

Description.—A single slightly deformed, fragmentary phragmocone, 8.5 mm in length and approximately 1.8 mm in diameter near its adoral end; conch longiconic producing slight curvature, cross section circular and expansion gradual; shell wall longitudinally fluted with ridges and concave interspaces; crests of ridges may be granular; concave septa shallow; camerae relatively short.

Material examined.—AMNH 6113.

Discussion.—Siphuncular structure of the specimen has not been preserved, but it is tentatively placed in *Cyrtothoracoceras* because its external characters resemble those of *C. dombarense* Shimansky, 1968, from the lower Carboniferous in the southern Urals.

Genus ***Dolorthoceras*** Miller, 1931

Type species.—*Dolorthoceras circulare* Miller, 1931.

Dolorthoceras boggyense sp. nov.

Figures 3D, 7

Dolorthoceras n. sp., Smith, 1938, p. 6, pl. 1, figs. 13, 14.

? *Pseudorthoceras* sp., Fisher and Teichert, 1969, p. 11 (part), pl. 1, fig. 2.

Mooreoceras normale Miller, Dunbar and Condra, 1933. Crick, 1982, pl. 1, fig. 8.

Orthoconic nautiloid, Seuss *et al*., 2012a, fig. 3H.

Diagnosis.—Species of *Dolorthoceras* with dorsoventrally depressed cross section in apical shell; sutures oblique; cameral length moderate to short with maximum width/length ratios of 2.4–3.6; septal necks short, suborthochoanitic on ventral and cyrtochoanitic on dorsal side; cameral deposits episeptal-mural.

Description.—Conchs longiconic orthocones with gradual to moderate expansion, whose angle is 5–6° in lateral view of post-embryonic shells; cross sections of conchs are dorsoventrally depressed in apical shells, then become circular; shell surface lacks ornamentation; holotype is imperfect phragmocone, 31.5 mm in length and 6.9 mm in dorsoventral diameter near apical end; largest specimen (paratype, AMNH 5953) is imperfect phragmocone approximately 9 mm in diameter; no peristome preserved. Embryonic shells have asymmetrical profile in lateral view, with rounded apex that faintly shifts to ventral(?) side; nepionic constriction occurs at distance of 8.4 mm (paratype, AMNH 5927) and 9.2 mm (paratype, AMNH 5920) from apex; except for apical portion that expands approximately 20° in angle, embryonic shells are nearly cylindrical. Sutures oblique, inclining dorsally with approximate angle of 6–8° for vertical plane to conch axis; septal curvature is moderate with narrow furrow on mid-dorsal region; camerae moderate to short in length; maximum width/length ratios of camera are 2.4–3.6; siphuncle central in position, then shifts ventrally and becomes subcentral in more adoral positions in the conch; siphuncular position ratios (distance of central axis of septal foramen from ventral shell surface per corresponding dorsoventral conch diameter) are 0.48–0.50; siphuncular wall consists of asymmetrical septal necks and thin connecting rings; shapes of septal necks are suborthochoanitic on ventral and cyrtochoanitic on dorsal side; length of septal necks is short, ranging from 0.15 to 0.23 mm in holotype; connecting rings subcylindrical with abrupt constrictions at septal foramina. Endosiphun-

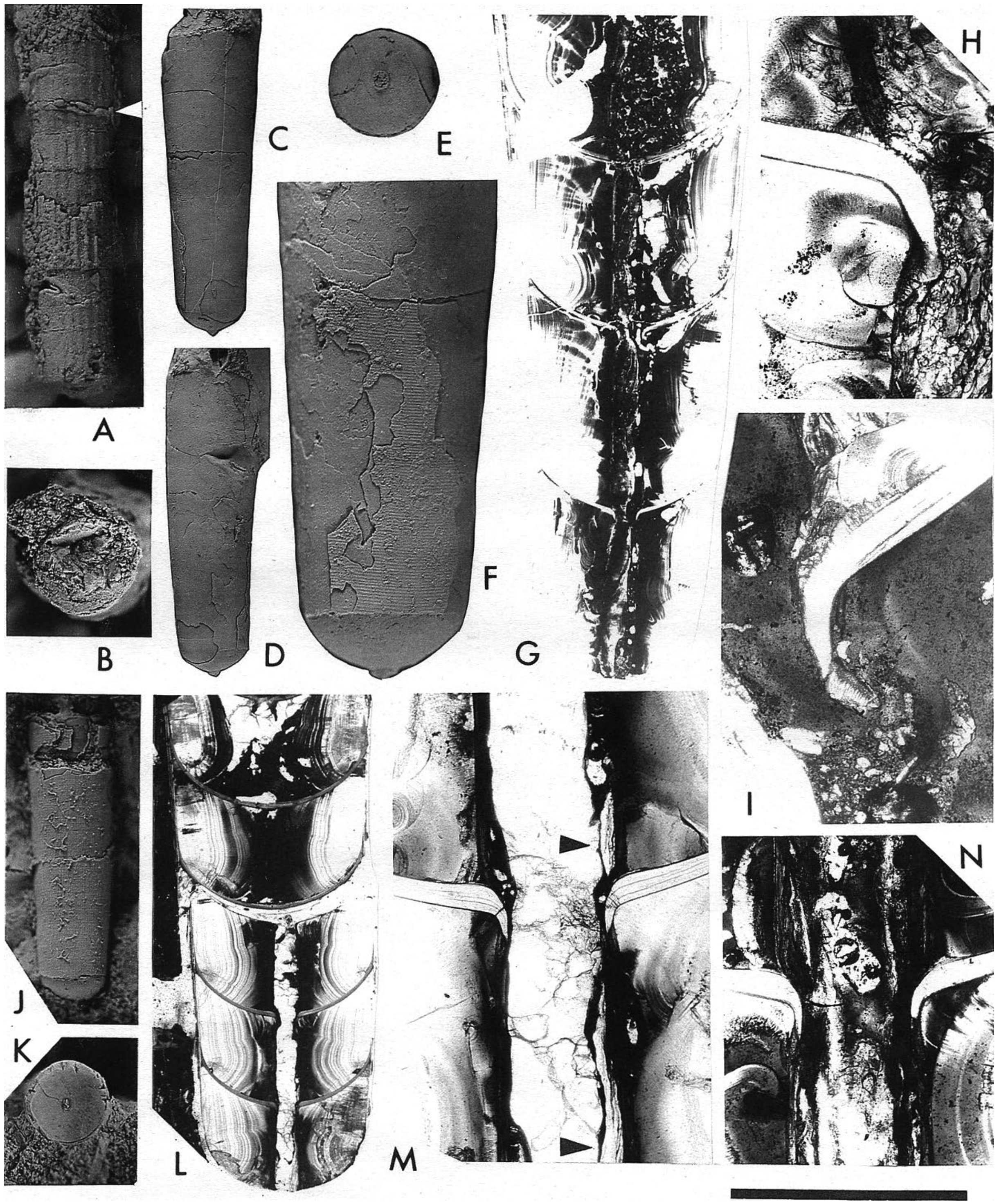

Figure 6. **A, B,** *Cyrtothoracoceras*? sp., AMNH 6113; A, lateral view; B, septal view. Arrow in A indicates position of B. **C–I,** *Unklesbayoceras striatulum* gen. et sp. nov., holotype, AMNH 6114; C, dorsal view; D, lateral view, venter on right; E, septal view of apical end, venter down; F, partial enlargement to show details of surface ornamentation, ventral view; G, dorsoventral thin section, venter on left; H, partial enlargement of G to show details of ventral septal neck; I, partial enlargement of G to show details of dorsal septal neck. **J–M,** *Sueroceras oklahomense* (Smith, 1938); J, AMNH 5994, side view; K, AMNH 5992, septal view, conch orientation uncertain; L, M, AMNH 5996; L, dorsoventral thin section, venter on right; M, partial enlargement of L, showing details of siphuncle. **N,** *Arbuckleoceras tricamerae* (Smith, 1938), partial enlargement of Figure 4K to show details of siphuncle. Arrows in M indicate endosiphuncular deposits. Scale bar is 5.7 mm in A; 4 mm in B, L; 20 mm in C, D; 10 mm in E; 8 mm in F, G, J, K; 0.8 mm in H, I, M, N.

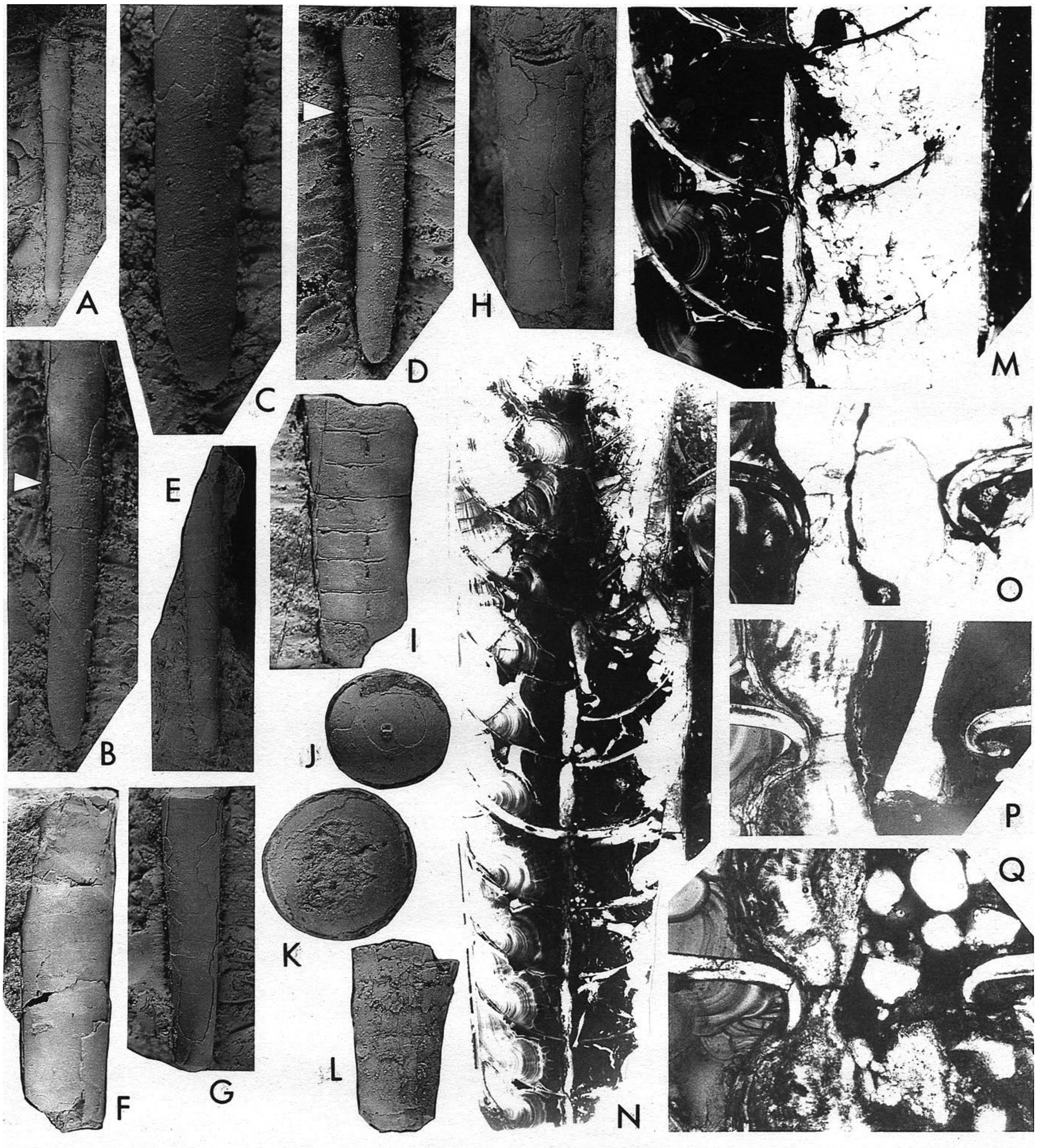

Figure 7. *Dolorthoceras boggyense* sp. nov. **A–C,** paratype, AMNH 5920; A, lateral view, venter on right?; B, C, partial enlargements of apical shell; **D,** paratype, AMNH 5927, lateral view, venter on right?; **E,** paratype, AMNH 5922, side view; **F, N, P, Q,** holotype, AMNH 5918; E, lateral view, venter on right; N, dorsoventral thin section, venter on left; P, Q, partial enlargements of N to show details of septal necks; **G,** paratype, AMNH 5926, lateral view, venter on left; **H,** paratype, AMNH 5919, ventral view; **I,** paratype, AMNH 5925, dorsal view, note septal furrows; **J,** paratype, AMNH 5924, septal view, venter down; **K, L,** paratype, AMNH 5953; K, septal view, venter down; L, dorsal view; **M, O,** partial enlargements of Figure 3D to show details of cameral and endosiphuncular deposits and septal neck. Arrows indicate nepionic constrictions. Scale bar is 20 mm in A, E–H, L; 8 mm in B, D, N; 4 mm in C, M; 10 mm in I–K; 0.8 mm in O–Q.

cular deposits form continuous lining on ventral siphuncular wall; cameral deposits are ventrally thicker than dorsally, episeptal-mural.

Material examined.—Holotype, AMNH 5918. Paratypes, AMNH 5915–5917, 5919–5922, 59245–5927, 5953. In addition, 27 specimens, AMNH 5914, 5923, 5928–5952, are assigned to *Dolorthoceras boggyense* sp. nov.

Etymology.—The specific name is derived from the type stratum, called the Boggy Formation.

Discussion.—A comparable species, *Dolorthoceras medium* Gordon (1957, p. 23, pl. 2, figs. 14, 21) from the Upper Mississippian Alapah Limestone of Alaska, with *D. boggyense* sp. nov. differs in having nearly straight sutures and well developed hyposeptal deposits. A single examined specimen of *Dolorthoceras* n. sp. in Smith (1938) of 21 mm diameter probably represents the more adoral portion of the new species than the specimens examined here.

Genus ***Smithorthoceras*** gen. nov.

Type species.—*Orthoceras unicamera* Smith, 1938, by monotypy.

Diagnosis.—Conch longiconic orthocone with circular cross sections and very gradual expansion; shell surface ornamented by transverse lirae; deeply curved septa form directly transverse sutures and long camerae; siphuncle central; septal necks orthochoanitic and very long, whose apical tips are weakly bent outwards; connecting rings cylindrical; parietal endosiphuncular deposits partly form continuous lining; cameral deposits episeptal and mural.

Etymology.—The generic name is a combination of the late H. J. Smith, who described cephalopods from the Buckhorn Asphalt Quarry for the first time, and *Orthoceras* indicating this is an orthoconic cephalopod.

Discussion.—Cameral and siphuncular characters of *Smithorthoceras* gen. nov. are unique for pseudorthoceratids, and for that reason, they suggest relationships with some orthoceratid genera, including *Michelinoceras* Foerste, 1932, *Mericoceras* Zhuravleva, 1978, and *Trematoceras* Eichwald, 1851. However, the presence of endosiphuncular deposits is an exclusive morphological feature restricted to the Pseudorthoceratidae. We think that similarities between *Smithorthoceras* and the above-mentioned three orthoceratid genera are the results of convergent evolution in the two separate lineages.

The cylindrical connecting rings of *Smithorthoceras* warrant its placement in the Spyroceratinae. Within the subfamily, *Smithorthoceras* has a surficial ornamentation similar to that seen in *Mitorthoceras* Gordon, 1960. However, the latter Late Mississippian genus differs in having a supracentral siphuncular position with suborthochoanitic septal necks (Niko and Mapes, 2015).

Smithorthoceras unicamera (Smith, 1938)

Figures 3K, 8

Orthoceras unicamera Smith, 1938, p. 7, pl. 1, figs. 1–3.
Michelinoceras directum Unklesbay, 1962, p. 19, pl. 1, figs. 1–3.
"*Orthoceras*" *unicamera* Smith. Fisher and Teichert, 1969, p. 11, pl. 1, fig. 1, pl. 2, figs. 2, 3, pl. 3, fig. 3, text-figs. 3A–D, 4A, B, 5A–J; Ristedt, 1971, pl. 31, figs. 1, 3, 5, 6, pl. 32, figs. 2, 4–6, pl. 33, figs. 2, 4–9, pl. 34, fig. 1, pl. 35, figs. 2, 4, 6, pl. 36, figs. 2, 5–8, pl. 38, figs. 4, 5, 8, pl. 39, figs. 7, 8, pl. 40, figs. 1, 3, 5, 6, pl. 41, figs. 4–7, pl. 42, fig. 3, text-fig. 6.
Mitorthoceras crebriliratum (Girty, 1909). Crick, 1982, pl. 1, figs. 3, 6, 7, 11, 12.
Mitorthoceras girty [*sic*] Gordon, 1964. Crick, 1982, pl. 1, fig. 9.
Mitorthoceras perfilosum Gordon, 1964. Crick, 1982, pl. 1, figs. 10, 13.
Michelinoceras? *unicamera* (Smith). Sturgeon *et al*., 1997, p. 18, pl. 1-1, figs. 1–7.
Orthoconic nautiloid, Seuss *et al*., 2012a, figs. 3A, B, D–G.

Description.—Longiconic orthocones with circular cross sections and very gradual conch expansion, approximately 2° in angle; shell surface ornamented by transverse lirae that faintly incline toward venter; there are 9–15 lirae per 1 mm and at conch diameter of approximately 4 mm; peristome and embryonic shell are unknown. Sutures directly transverse; camerae long with maximum width/length ratios of 1.1–1.2; septal curvature deep; siphuncle central in position; siphuncular wall consists of orthochoanitic septal necks and thin connecting rings; apical tips of septal necks weakly bent outwardly; septal necks are very long, 0.85–0.93 mm at conch diameter of approximately 5 mm; ventral septal neck thicker than dorsal one; shapes of connecting rings are cylindrical. Endosiphuncular deposits parietal, forming discontinuous lining on ventral siphuncular wall; cameral deposits differentiated into episeptal and mural.

Material examined.—AMNH 5954–5976.

Discussion.—In addition to the type locality Buckhorn Asphalt Lagerstätte, this species is also recorded from the Desmoinesian of eastern Ohio (Sturgeon *et al*., 1997).

Genus ***Sueroceras*** Riccardi and Sabattini, 1975

Type species.—*Sueroceras irregulare* Riccardi and Sabattini, 1975.

Discussion.—Although the subfamilial assignment of *Sueroceras* was not determined by Riccardi and Sabattini (1975), its suborthochoanitic septal necks and subcylindrical to fusiform connecting rings indicate that the genus is undoubtedly placed in the Spyroceratinae.

Sueroceras oklahomense (Smith, 1938)

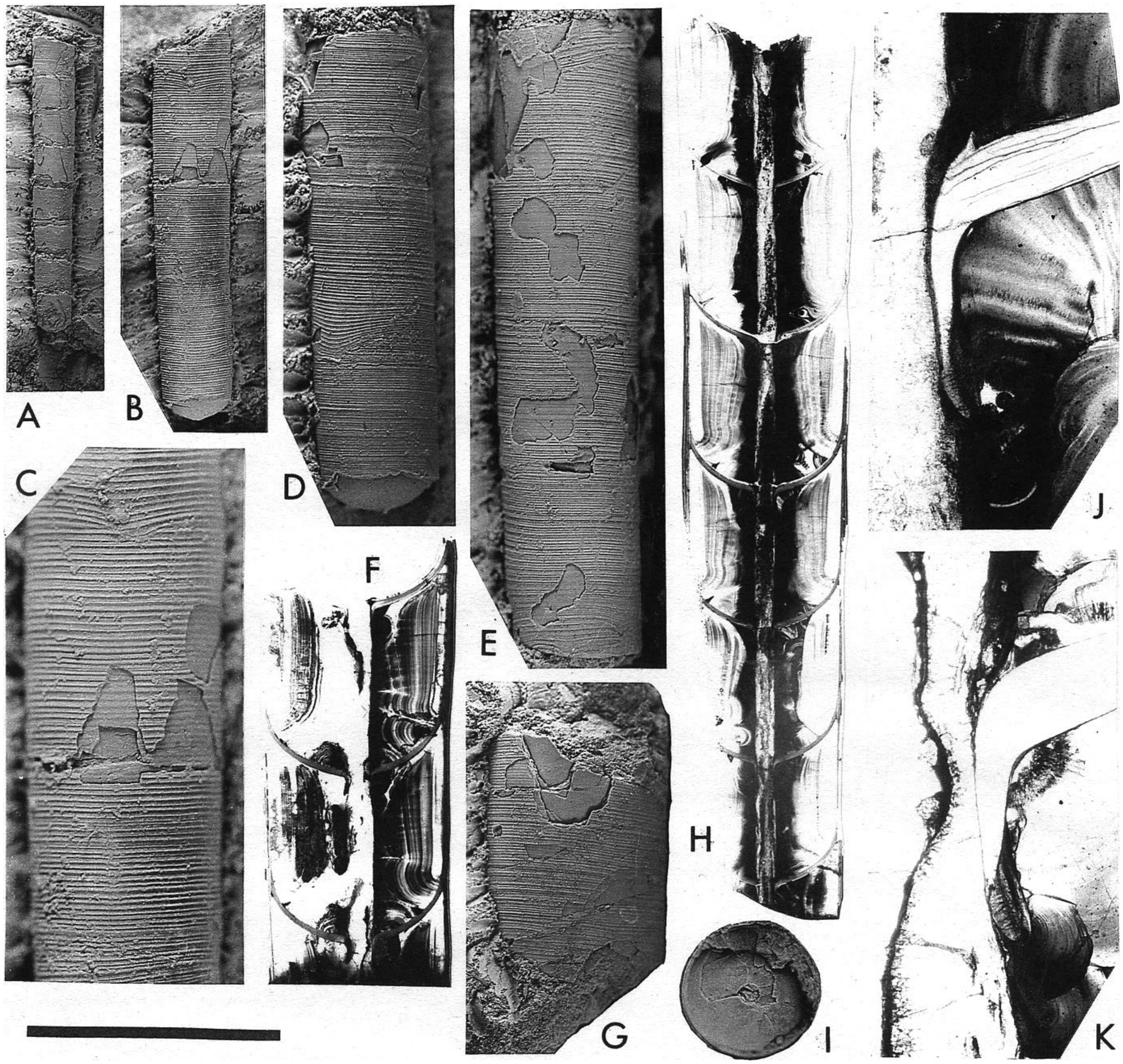

Figure 8. *Smithorthoceras unicamera* (Smith, 1938). **A,** ASMN 5954, side view; **B, C, I,** ASMN 5960; B, ventral view; C, partial enlargement of B to show details of surface ornamentation; I, septal view of apical end, venter down; **D,** ASMN 5961, lateral view, venter on right; **E,** ASMN 5957, lateral view, venter on right; **F, K,** ASMN 5956; F, dorsoventral thin section, venter on right; K, partial enlargement of F to show details of ventral septal neck and endosiphuncular deposits; **G,** ASMN 5976, lateral view of body chamber, venter on right; **H, J,** ASMN 5958; H, dorsoventral thin section, venter on left; J, partial enlargement of H to show details of dorsal septal neck. Scale bar is 20 mm in A, B, G; 8 mm in C–F, H; 10 mm in I; 0.8 mm in J, K.

Figures 5C, 6J–M

Dolorthoceras oklahomense Smith, 1938, p. 6, pl. 1, figs. 15, 16; Gordon, 1964, p. 119, 120.; Sabattini *et al*., 2006, p. 1144.

Cancellate "*Orthoceras*", Fisher and Teichert, 1969, p. 12, pl. 1, fig. 3, pl. 2, fig. 1.

Kionoceras? sp., Ristedt, 1971, pl. 28, fig. 5, pl. 30, figs. 1–5, pl. 31, figs. 4, 7.

Dolorthoceras oklahomense?. Crick, 1982, pl. 1, fig. 2.

Kionoceras sp., Blind, 1987, pl. 1, fig. 4, pl. 3, fig. 3, text-figs. 2, 6, 7; 1988, text-figs. 1, 5, 7E, 9C; Tanabe and Uchiyama, 1997, fig. 10A–E.

Description.—Examined specimens of small fragmentary phragmocones are longicones with circular cross sections; conch expansion is gradual, approximately 5° in angle; shell surface marked by fine cancellate ornamentation; peristome and embryonic shell are unknown. Sutures directly transverse; cameral length moderate for the family, maximum width/length ratios of 2.0–2.3; siphuncle nearly central in position; siphuncular wall consists of orthochoanitic septal necks and thin connecting rings; length of septal necks short, 0.21–0.22 mm at approximate conch diameter of 3 mm; shapes of connecting rings are cylindrical with weak constrictions at septal foramina. Endosiphuncular deposits are weak; thin parietal deposits developed on ventral siphuncular wall; cameral deposits mural.

Material examined.—AMNH 5992–5996.

Discussion.—Judging from their morphologies described above, the newly collected specimens are conspecific with *Dolorthoceras oklahomense* described from the same locality by Smith (1938). Herein, we classify *D. oklahomense* within *Sueroceras* because of possession of the cancellate surface ornamentation. Sabattini *et al*. (2006) previously suggested the possibility of the same reassignment.

Genus ***Sulphurnites*** gen. nov.

Type species.—*Sulphurnites taffi* sp. nov., by monotypy.

Diagnosis.—Conch longiconic orthocone with circular cross sections and gradual expansion; shell surface lacks ornamentation; septa deeply concave; camera relatively long to moderate in length; sutures directly transverse; siphuncle nearly central; septal necks short and suborthochoanitic; connecting rings subcylindrical to fusiform; endosiphuncular deposits initiate at apical and adoral junctions between septal neck and connection ring, then they mainly grow posteriorly and anteriorly; cameral deposits episeptal-mural and hyposeptal.

Etymology.—The generic name is derived from the rural community of Sulphur, Murray County, South-central Oklahoma. The type locality is situated approximately 10 km south of the outskirts of this community.

Discussion.—Endosiphuncular deposits of *Sulphurnites* gen. nov. are unique for the family Pseudorthoceratidae (see also Seuss *et al*., 2012a, figs. 7A1, 7A2, 7B, 7C2–6), whose incipient deposits mostly occur on septal necks. Similar deposits are also known from the Ordovician genus, *Mysterioceras* Teichert and Glenister, 1953, whose incipient deposits originate immediately behind septal necks. Except for the endosiphuncular deposits, the characters of *Sulphurnites* clearly correspond to those of the Spyroceratinae.

Sulphurnites taffi sp. nov.

Figure 3E, F, H–J

Orthoconic nautiloid, Seuss *et al*., 2012a, figs. 2, 4A–F, 5A–F, 6A–F, 7A1, 7A2, 7B, 7C1–6.

Orthoconic nautiloid (Pseudorthoceratidae gen. et sp. indet.), Seuss *et al*., 2012b, figs. 3, 4A, B, 6A–C, 7A–H, 8B–D.

Diagnosis.—As for the genus.

Description.—Both available specimens are imperfect phragmocones, which are longiconic orthocones with circular cross sections and unornamented shell surface; expansion angle of conch is gradual, approximately 4°; the holotype is 43.5 mm in length and 8.1 mm in diameter near its adoral end; a paratype attains approximately 22 mm in diameter; no peristome and no embryonic shell preserved. Sutures directly transverse; cameral length relatively long to moderate for the family with maximum width/length ratios of 1.7–2.0; septa deeply concave; siphuncle nearly central in position; siphuncular wall consists of suborthochoanitic septal necks and thin connecting rings; outward curvature of septal necks is faint; length of septal necks is short, ranging from 0.52 to 0.61 mm in the holotype; connecting rings exhibit weak inflations in camerae and distinct constrictions at septal foramina, forming subcylindrical to fusiform profiles. Incipient parts of endosiphuncular deposits occur at apical and adoral junctions between septal neck and connecting ring on ventral siphuncular wall; among them, apical deposits mainly extend posteriorly and adoral ones mainly extend anteriorly; surface of septal necks and dorsal siphuncular wall are not covered by endosiphuncular deposits; cameral deposits well developed, differentiated into episeptal-mural and hyposeptal.

Material examined.—Holotype, AMNH 5997. Paratype, BSPG 2011 0002.

Etymology.—This species is named in honor of the late J. A. Taff in recognition of his contributions to the geology in Oklahoma.

Discussion.—Weak conch curvature is obscure in the examined fragmentary specimens. Thus, in such material *Sulphurnites taffi* sp. nov. shares similar external characters with an associated species, *Arbuckleoceras tricamerae* (Smith, 1938; see above). However, the latter species can be distinguished by the presence of cylindrical connecting rings and the absence of hyposeptal deposits.

Genus ***Unklesbayoceras*** gen. nov.

Type species.—*Unklesbayoceras striatulum* sp. nov. by monotypy.

Diagnosis.—Conchs longiconic with weak endogastric curvature, moderate expansion and circular cross sections; shell surface ornamented by transverse lirae; sutures directly transverse; camerae long to relatively long; siphuncle nearly central and supracentral in position; septal necks long and suborthochoanitic; connecting rings cylindrical with constrictions at septal foramina; endosiphuncular deposits form thick lining on ventral siphuncular wall; cameral deposits episeptal-mural.

Etymology.—The generic name is to honor the late A. G. Unklesbay, in recognition of his contributions to the study of upper Paleozoic cephalopods in North America.

Discussion.—*Unklesbayoceras* gen. nov. has several synapomorphies found with the Spyroceratinae, such as suborthochoanitic septal necks and cylindrical connecting rings. Of the genera included in this subfamily, *Unklesbayoceras* exhibits similarities with the Mississippian genus *Mitorthoceras* Gordon, 1960 (see Niko and Mapes, 2015 for the emended diagnosis of the genus). However, the new genus differs from *Mitorthoceras* in having weak endogastric curvature of the conch, longer camerae and a less eccentric siphuncular position.

Unklesbayoceras striatulum sp. nov.

Figure 6C–I

Diagnosis.—As for the genus.

Description.—Longiconic conch with weak endogastric curvature and circular cross section; conch expansion of approximately 6° is moderate for the family; the holotype only known specimen of an imperfect phragmocone is 26.0 mm in length and 6.1 mm in apical diameter; shell surface ornamented by weak transverse lirae that faintly incline toward venter; there are 9–15 lirae at a conch length of 1 mm; body chamber and embryonic shell not preserved. Sutures directly transverse, except for narrow dorsal furrow; septal concave curvature is relatively deep; camerae long to relatively long for the family, indicating form ratios (maximum width/length) of 1.1–1.5; siphuncle near central axis of conch and faintly supracentral; siphuncular position ratio (distance of central axis of septal foramen from ventral shell surface per corresponding conch diameter) is 0.53; siphuncular wall consists of suborthochoanitic septal necks and thin connecting rings; length of septal necks is long, 0.52–0.75 mm; shapes of connecting rings are cylindrical with constrictions at septal foramina. Endosiphuncular deposits well developed, to form thick lining on ventral siphuncular wall; thin parietal deposits developed on ventral siphuncular wall; cameral deposits episeptal-mural.

Etymology.—The specific name is derived from the Latin, *striatulus* (= having weak lirae), referring to the surface ornamentation.

Material examined.—Holotype, AMNH 6114.

Discussion.—This species is represented by a single, well preserved specimen. Its distinctive features including endogastric conch curvature, cameral nature and siphuncular position are sufficiently pronounced to warrant establishing a new genus and species.

Significance

Cephalopods of the Buckhorn Asphalt Lagerstätte have been investigated for biogeochemistry (Crick, 1982; Brand, 1987, 1989; Sadd, 1991; Seuss *et al*., 2012a), shell ultrastructure (Ristedt, 1971; Blind, 1988, 1991), ultrastructure of organic remnants (Grégoire, 1988), apical shell characters (Ristedt, 1971; Blind, 1987, 1988; Tanabe and Uchiyama, 1997), and the structure of cameral and endosiphuncular deposits (Fischer and Teichert, 1969; Crick, 1982; Seuss *et al*., 2012b). However, the taxonomy of the cephalopods analyzed in these papers has never been revised or treated in detail. Our detailed study of the orthocerids from this Lagerstätte indicates that nine species representing nine genera are present. They include five previously described species by McChesney (1859) and Smith (1938) and four so far undescribed species. Furthermore, the generic placement of these species is reevaluated to conform to current taxonomic standards.

Pennsylvanian orthocerid cephalopod faunas are poorly known because they are considered to be poor biostratigraphic tools, and therefore, little effort has been undertaken to evaluate and describe this part of cephalopod faunas. Thus, this new taxonomic information gained from the Buckhorn Asphalt Lagerstätte is important to fill the knowledge gap of faunal constituents between the relatively well documented Mississippian and early Permian orthocerids. An additional reason why the Buckhorn Asphalt Lagerstätte is important is that it constitutes the oldest extensive cephalopod fauna that is still preserved in its original shell material, namely aragonite. For this reason the shells have provided important information, as indicated above, on late Palaeozoic cephalopods. In addition, this Desmoinesian fauna is extremely diverse in comparison with those of other regions of the world, including European Russia (Shimansky, 1968: 3 species in the Moscovian (= Atokan and Desmoinesian)), South China (Niko *et al*., 1997: 4 species in the Moscovian), and Southwest Japan (Niko *et al*., 1987; 1995: 5 species in the Moscovian). At the generic level there are new and probably endemic genera in the deposit, namely *Arbuckleoceras*, *Smithorthoceras*, *Sulphurnites* and *Unklesbayoceras*. They account for around half of the total generic number. This is also noteworthy because orthocerids were on the decline during the Pennsylvanian, and according to Sweet (1964), there were no new orthocerid genera at that time.

The Midcontinent area of North America was located at a low-latitude (5–10° N) region during the Middle to Late Pennsylvanian (e.g. Scotese and McKerrow, 1990; Scotese, 1997). Simultaneous sea level changes produced transgressions and regressions triggered by forming and melting ice of Gondwanan glaciers (Algeo *et al*., 2008). In North America, these sea level changes formed the Midcontinent Sea (Heckel, 1994), in which the sediments of the Buckhorn Asphalt Lagerstätte were deposited. The sea opened westward and had a connection to the Panthalassa Ocean through narrow straits between the Milk River, the Ancestral Uncompahgre and the Amarillo-Wichita Uplifts (Algeo and Heckel, 2008). The high diversity and provincialism of the Desmoinesian orthocerid fauna we report from the Buckhorn Asphalt Lagerstätte were strongly influenced by these environments. There is a possibility that this tropical epeiric sea provided a habitat of refuge for Desmoinesian orthocerids, especially in the mountainous terrain that formed small, restricted basins in the Arbuckle Uplift where the Buckhorn Asphalt was deposited.

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References

Agassiz, L., 1847: *An Introduction to the Study of Natural History, in a Series of Lectures Delivered in the Hall of the College of Physicians and Surgeons*, 58 p. Greeley and McElrath, New York.

Algeo, T. J. and Heckel, P. H., 2008: The Late Pennsylvanian Midcontinent Sea of North America: A review. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 268, p. 205–221.

Algeo, T. J., Rowe, H., Hower, J. C., Schwark, L., Herrmann, A. and Heckel, P. H., 2008: Changes in ocean denitrification during Late Carboniferous glacial-interglacial cycles. *Nature Geoscience*, vol. 1, p. 709–714.

Blind, W., 1987: Vergleichend morphologische und schalenstrukturelle Untersuchungen an Gehäusen von *Nautilus pompilius*, *Orthoceras* sp., *Pseudorthoceras* sp. und *Kionoceras*. sp. *Palaeontographica*, *Abteilung A*, Band 198, p. 101–128, pls. 1–4.

Blind, W., 1988: Comparative investigations on the shell morphology and structure of *Nautilus pompilius*, *Orthoceras* sp., *Pseudorthoceras* sp. and *Kionoceras*. sp. (Zur Schalenstruktur von *Nautilus pompilius*, *Orthoceras* sp., *Pseudorthoceras* sp. und *Kionoceras*. sp.). *In*, Wiedmann, J. and Kullmann, J. *eds*., *Cephalopods: Present and Past. Second International Cephalopod Symposium, O. H. Schindewolf Symposium, Tübingen, 1985*, p. 273–289. E. Schweizerbart'sche (Nägele u. Obermiller), Stuttgart.

Blind, W., 1991: Über Anlage und Funktion von Kammerablagerungen in Orthoceren-Gehäusen. *Palaeontographica*, *Abteilung A*, Band 218, p. 35–47, pls. 1–6.

Brand, U., 1987: Biogeochemistry of nautiloids and paleoenvironmental aspects of Buckhorn seawater (Pennsylvanian), southern Oklahoma. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 61, p. 255–264.

Brand, U., 1989: Aragonite-calcite transformation based on Pennsylvanian molluscs. *Geological Society of American Bulletin*, vol. 101, p. 377–390.

Bruguière, J. G., 1789: *Encyclopédie Méthodique. Histoire Naturelle des Vers*, *Tome Premier*, 757 p. Panckoucke, Paris and Liège.

Crick, R. E., 1982: The mode and tempo of cameral deposit formation: Evidence of orthoconic nautiloid physiology and ecology. *Third North American Paleontological Convention*, *Proceedings*, vol. 1, p. 113–118.

Eichwald, E. von, 1851: Naturhistorische Bemerkungen, als Beitrag zur vergleichenden Geognosie, auf einer Reise durch die Eifel, Tyrol, Italien, Sizilien und Algier. *Nouveaux Mémoires de la Société Imperiale de Naturalistes de Moscou*, vol. 9, p. 1–464.

Ernst, A., Seuss, B., Taylor, P. D. and Nützel, A., 2016: Bryozoan fauna of the Boggy Formation (Deese Group, Pennsylvanian) of the Buckhorn Asphalt Quarry, Oklahoma, USA. *Palaeobiodiversity and Palaeoenvironments*, vol. 96, p. 517–540.

Fisher, A. G. and Teichert, C., 1969: Cameral deposits in cephalopod shells. *University of Kansas*, *Paleontological Contributions*, *Paper*, 37, p. 1–30, pls. 1–4.

Flower, R. H., 1939: Study of the Pseudorthoceratidae. *Palaeontographica Americana*, vol. 2, p. 1–214, pls. 1–9.

Flower, R. H., 1962: Notes on the Michelinoceratida. New Mexico. *Bureau of Mines and Mineral Resources*, *Memoir*, 10, p. 19–42, pls. 4–6.

Flower, R. H. and Caster, K. E., 1935: The stratigraphy and paleontology of Northwestern Pennsylvania. Part II: Paleontology. Section A: The cephalopod fauna of the Conewango Series of the Upper Devonian in New York and Pennsylvania. *Bulletins of American Paleontology*, vol. 22, p. 199–271.

Foerste, A. F., 1932: Black River and other cephalopods from Minnesota, Wisconsin, and Ontario (Part I). *Denison University Bulletin*, *Journal of the Scientific Laboratories*, vol. 27, p. 47–136, pls. 7–37.

Gemmellaro, G. G., 1890: La fauna dei calcarì con *Fusulina* della valle del fiume Sosio (nella provincia di Palermo). *Giornale di Scienze Naturali ed Economiche Pubblicato per Cura della Società di Scienze Naturali ed Economiche di Palermo*, vol. 20, p. 37–138, pls. 11–19.

Girty, G. H., 1909: The fauna of the Caney Shale of Oklahoma. *United States Geological Survey*, *Bulletin*, 377, p. 1–106.

Girty, G. H., 1911: On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, vol. 21, p. 119–156.

Gordon, M. Jr., 1957: Mississippian cephalopods of northern and Eastern Alaska. *United States Geological Survey Professional Paper*, no. 283, p. 1–61, pls. 1–6.

Gordon, M. Jr., 1960: Some American Midcontinent Carboniferous cephalopods. *Journal of Paleontology*, vol. 34, p. 133–151, pls. 27–28.

Gordon, M. Jr., 1964: Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, no. 460, p. 1–322, pls. 1–30.

Grégoire, C., 1988: Organic remnants in shells of Cambrian nautiloids and in cameral deposits of Pennsylvanian nautiloids. *Senckenbergiana Lethaea*, vol. 69, p. 73–86.

Ham, W. E., 1969: *Regional Geology of the Arbuckle Mountains*, *Okla-*

homa: Oklahoma Geological Survey Guidebook 17, 52 p. University of Oklahoma, Norman.

Haniel, C. A., 1915: Die Cephalopoden der Dyas von Timor. *Paläontologie von Timor*, Band 3, p. 1–153, pls. 46–56.

Heckel, P. H., 1994: Evaluation of evidence for glacial-eustatic control over marine Pennsylvanian cyclothems in North America and consideration of possible tectonic effects. *In*, Dennison, J. M. and Ettensohn, F. R. *eds.*, *Tectonic and Eustatic Controls on Sedimentary Cycles*, p. 65–87. SEPM (Society for Sedimentary Geology) Special Publication, Concepts in Sedimentology and Paleontology, vol. 4, SEPM (Society for Sedimentary Geology), Tulsa.

Hemish, L. A. and Suneson, N. H., 1997: *Stratigraphy and Resources of the Krebs Group (Desmoinesian), South-Central Arkoma Basin, Oklahoma: Oklahoma Geological Survey Guidebook 30*, 83 p. University of Oklahoma, Norman.

Kröger, B. and Mapes, R. H., 2004: Lower Carboniferous (Chesterian) embryonic orthoceratid nautiloids. *Journal of Paleontology*, vol. 78, p. 560–573.

Kuhn, O., 1940: *Paläozoologie in Tabellen*, 50 p. Fischer, Jena.

McChesney, J. H., 1859: Descriptions of new species of fossils, from the Palaeozoic rocks of the western states. *Extra Transactions*, *Chicago Academy of Sciences*, vol. 1, p. 1–76.

M'Coy, F., 1844: *A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland*, 274 p. Privately published. (*reissued by Williams and Norgate, London, 1862*)

Miller, A. K., 1931: Two new genera of Late Paleozoic cephalopods from Central Asia. *American Journal of Science*, *Series 5*, vol. 22, p. 417–425.

Miller, A. K., 1944: Permian cephalopods. *In*, King, E. E., Dunbar, C. O., Cloud, P. E. Jr. and Miller, A. K., *Geology and Paleontology of the Permian Area Northwest of Las Delicoas*, *Southwestern Coahuila*, *Mexico*, p. 71–172, pls. 20-45. Geological Society of America Special Paper 52.

Miller, A. K., Dunbar, C. O. and Condra, G. E., 1933: The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey*, *Bulletin*, 9, p. 1–240, pls. 1–24.

Niko, S. and Mapes, R. H., 2015: Early Carboniferous nautiloids from the Ruddell Shale Member in Arkansas. Midcontinent North America. *Paleontological Research*, vol. 19, p. 52–60.

Niko, S. and Nishida, T., 1987: Early Permian cephalopods from the Mizuyagadani Formation, Fukuji district, Central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 146, p. 35–41.

Niko, S., Nishida, T. and Kyuma, Y., 1987: Middle Carboniferous Orthocerataceae and Pseudorthocerataceae (Mollusca: Cephalopoda) from the Akiyoshi Limestone, Yamaguchi Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 148, p. 335–345.

Niko, S., Nishida, T. and Kyuma, Y., 1995: A new Carboniferous cephalopod *Bogoslovskya akiyoshiensis* from Southwest Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 179, p. 193–195.

Niko, S., Nishida, T. and Kyuma, Y., 1997: Moscovian (Carboniferous) orthoconic cephalopods from Guizhou and Guangxi, South China. *Paleontological Research*, vol. 1, p. 100–109.

Riccardi, A. C. and Sabattini, N., 1975: Cephalopoda from the Carboniferous of Argentina. *Palaeontology*, vol. 18, p. 117–136.

Ristedt, H., 1971: Zum Bau der orthoceriden Cephalopoden. *Palaeontographica*, *Abteilung A*, Band 137, p. 155–195, pls. 28–42.

Rowland, T. L., Ham, W. E. and Squires, R. L., 1973: Stop 8. Deese (Desmoinesian) strata on Dry Branch of Buckhorn Creek, north-central part of sec. 26, T. 1S., R. 3 E., Murray County. Strike mostly N. 60° E., dip 32° NW. *In*, *Regional Geology of the ArbuckleMountains*, *Oklahoma*, p. 51–54. Geological Society of America, Guidebook for Field Trip No. 5, November 10-11, 1973, Oklahoma Geological Survey and the University of Oklahoma, Norman.

Sabattini, N., Riccardi A. C. and Pagani, M. A., 2006: Cisuralian cephalopods from Patagonia, Argentina. *Journal of Paleontology*, vol. 80, p. 1142–1151.

Sadd, J. L., 1991: Tectonic influences on carbonate deposition and diagenesis, Buckhorn Asphalt, Deese Group (Desmoinesian), Arbuckle Mountains, Oklahoma. *Journal of Sedimentary Petrology*, vol. 61, p. 28–42.

Scotese, C. R., 1997: *Palaeogeographic Atlas, Paleomap Progress Report 90-0497*, 37 p. University of Texas, Arlington.

Scotese C. R. and McKerrow, W. S., 1990: Revised world maps and introduction. *In,* McKerrow, W. S. and Scotese C. R. *eds.*, *Palaeozoic Palaeogeography and Biogeography*, p. 1–21. Geological Society Memoir, no. 12.

Seuss, B., Mapes, R. H., Klug, C. and Nützel, A., 2012a: Exceptional cameral deposits in a sublethally injured Carboniferous orthoconic nautiloid from the Buckhorn Asphalt Lagerstätte in Oklahoma, USA. *Acta Palaeontologica Polonica*, vol. 57, p. 375–390.

Seuss, B., Nützel, A., Mapes, R. H. and Yancey, T. E., 2009: Facies and fauna of the Pennsylvanian Buckhorn Asphalt Quarry deposits: a review and new data on an important Palaeozoic fossil *Lagerstätte* with aragonite preservation. *Facies*, vol. 55, p. 609–645.

Seuss, B., Titschack, J., Seifert, S., Neubauer, J. and Nützel, A., 2012b: Oxygen and stable carbon isotopes from a nautiloid from the middle Pennsylvanian (Late Carboniferous) impregnation *Lagerstätte* 'Buckhorn Asphalt Quarry' –Primary paleo-environmental signals versus diagenesis. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 319–320, p. 1–15.

Shimansky, N., V., 1954: Straight Nautiloidea and Bactritoidea of the Sakmarian and Artinskian stages of the southern Urals. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, vol. 44, p. 1–156, pls. 1–12. (*in Russian; original title translated*)

Shimansky, V. N., 1968: Carboniferous Orthoceratida, Oncoceratida, Actinoceratida and Bactritida. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, vol. 117, p. 1–151, pls. 1–20. (*in Russian; original title translated*)

Shimizu, S. and Obata, T., 1935: New genera of Gotlandian and Ordovician nautiloids. *Journal of the Shanghai Science Institute*, *Section 2*, *Geology*, *Palaeontology*, *Mineralogy*, *and Petrology*, vol. 2, p. 1–10.

Shimizu, S. and Obata, T., 1936: Remarks on Hayasaka's *Protocycloceras* cfr. *cyclophorum* and the Permian and Carboniferous orthoconic nautiloids of Asia. (Résumé.). *Journal of the Geological Society of Japan*, vol. 43, p. 11–29. (*in Japanese with English abstract*)

Smith, H. J., 1938: *The Cephalopod Fauna of the Buckhorn Asphalt*, 40 p. University of Chicago Libraries, Chicago.

Squires, R. L., 1973: *Burial environment, diagenesis, mineralogy, and Mg and Sr contents of skeletal carbonates in the Buckhorn Asphalt of Middle Pennsylvanian age, Arbuckle Mountains, Oklahoma*. Thesis for Degree of Doctor of Philosophy, 226 p. California Institute of Technology, Pasadena.

Sturgeon, M. T., Windle, D. L., Mapes, R. H. and Hoare, R. D., 1997: Pennsylvanian cephalopods of Ohio. Part 1. Nautiloid and bactritoid cephalopods. *Ohio Division of Geological Survey*, *Bulletin*, 71, p. 1–191.

Sweet, W. C., 1964: Nautiloidea—Orthocerida. *In*, Moore, R. C. *ed*., *Treatise on Invertebrate Paleontology*, *Part K, Mollusca 3*, p. K216–K261. Geological Society of America, New York and Uni-

versity of Kansas Press, Lawrence.
Taff, J. A., 1899: Geology of the McAlester-Lehigh coal field, Indian Territory. *Nineteenth Annual Report of the United States Geological Survey to the Secretary of the Interior 1897–98*, *Part III–Economic Geology*, p. 429–456.
Tanabe, K. and Uchiyama, K., 1997: Development of the embryonic shell structure in *Nautilus*. *Veliger*, vol. 40, p. 203–215.
Teichert, C. and Glenister, B. F., 1953: Ordovician and Silurian cephalopods from Tasmania, Australia. *Bulletins of American Paleontology*, vol. 34, p. 1–66, pls. 1–6.
Turner, J. S., 1954: On the Carboniferous nautiloids: Some middle Viséan species from the Isle of Man. *Liverpool and Manchester Geological Journal*, vol. 1, p. 298–325, pls. 20–25.
Unklesbay, A. G., 1962: Pennsylvanian cephalopods of Oklahoma. *Oklahoma Geological Survey*, *Bulletin*, 96, p. 1–150, pls. 1–19.
Zhuravleva, F. A., 1978: Devonian orthocerids Super Order Orthoceratoidea. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, vol. 168, p. 1–223. (*in Russian; original title translated*)