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Solenochilus Springeri (White & St. John, 1868) from the Pennsylvanian of Southern Iowa

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Abstract. The unique Pennsylvanian nautilid *Solenochilus springeri* is described with reference to material from the lower Cherokee Group (Atokan or Desmoinesian) of Marion County, Iowa, and the Bloyd Formation (Morrowan) of northwestern Arkansas. The species was based originally on a specimen, now lost, from Adair County, Iowa; a neotype is selected from the Marion County collections. The detailed morphology of the pair of dorsolateral spines which characterize mature *Solenochilus* is described for the first time. These spines, whose length approximates the width of the mature body chamber, are hollow throughout. Each spine originated as a lateral expansion of a prominent dorsolateral ridge located on the umbilical shoulder.

INTRODUCTION

The Order Nautilida constitutes a group of coiled or curved cephalopods which appeared in the Early Devonian and includes most representatives of the Subclass Nautiloidea from the Carboniferous to the Recent. Many possess prominent sculpture, especially ventrolateral nodes and lateral ribs. One Permian nautilid, *Cooperoceras* Miller 1945, is characterized by the development of a paired series of long curved ventrolateral spines. The present study is a consideration of the occurrence, in Iowa, of a unique group of Late Paleozoic nautilids which developed a single pair of long dorsolateral spines at maturity. Represent-

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atives of this group from southern Iowa are from Pennsylvanian strata, and are referred to *Solenochilus* Meek & Worthen 1870. The single specimen which served for the erection of the type species of *Solenochilus [Nautilus (Cryptoceras) Springeri* White & St. John, 1868] was collected in Adair County, Iowa.

Solenochilus and *Acanthonautilus* Foord 1896 constitute the Family Solenochilidae Hyatt 1893, which is widely distributed in strata ranging in age from Late Mississippian through Early Permian. *Acanthonautilus,* the ancestral representative from the Mississippian, resembles *Solenochilus* in the gross form of the conch and ventral marginal position of the siphuncle. However, at least most Mississippian solenochilids differ from those of the Pennsylvanian and Permian by their more nearly tubular siphuncle and shorter septal necks (Furnish & Glenister, 1964, p. K441-K442, fig. 320). *Permonautilus* Kruglov 1933, from the Late Permian of the Soviet Union, is the only other nautilid genus known to possess a pair of spines similar to those of the Solenochilidae. Although that genus is imperfectly known, it has a subcentral siphuncle and consequently is referred to the nautilid Family Liroceratidae.

Historical Résumé

The first reference to the nautilids now included in *Solenochilus* was the erection of *Nautilus (Cryptoceras) Springeri* by White & St. John (1868) in Volume 1 of Transactions of the Chicago Academy of Sciences. This species, apparently based originally on a single specimen, was recorded from the "Upper coal measures of Adair County, Iowa". It was secured during the course of the early investigations of the Iowa Geological Survey, covering the period 1866-1869. The work was under the direction of Charles A. White, State Geologist, in collaboration with Orestes H. St. John, Assistant, and was published in two volumes as the "Report on the Geological Survey of the State of Iowa" (White, 1870). Under the law by which the Geological Survey of Iowa was reorganized, all of the type specimens were to be "deposited in the cabinet of the State University at Iowa City" (White & St. John, 1868, p. 115). However, the eventual disposition of most of the collections is unknown, and no trace of the holotype of *Solenochilus springeri* can be found in the present collections of the University of Iowa.

The nautilids now referred to *Solenochilus springeri* were originally placed in the subgenus *Cryptoceras* d'Orbigny 1850. *Cryptoceras* d'Orbigny is a homonym of *Cryptoceras* Barrande 1846, although the latter is a *nomen nudum* for which the valid name is *Ascoceras* Barrande 1847. Meek & Worthen (1870), recognizing the unsuitability of the name *Cryptoceras* for nautilids, pro-

posed the subgenus *Solenochilus* and designated *Nautilus (Cryptoceras) Springeri* as type species. The literal derivation of their subgeneric name is "channel lip", a reference to the contours of the spout-like base of the spine. Hyatt (1893) erected the Solenochilidae; he and several subsequent authors have referred, incorrectly, to "*Solenocheilus*" and the "Solenocheilidae".

Since the initital description of *Nautilus (Cryptoceras) Springeri, Solenochilus* has proved to be of cosmopolitan distribution in nautiloid faunas of Pennsylvanian and Early Permian age (*e.g.* Miller & Owen, 1934; Miller & Youngquist, 1949). Numerous publications (*e.g.* Gordon, 1965) refer to *Solenochilus* in Mississippian strata. Many of these Mississippian taxa are better referred to the ancestral genus *Acanthonautilus* (Furnish & Glenister, 1964), although clarification of the temporal relations between the two solenochilid genera must await detailed study of a host of inadequately known species from the Soviet Union, Great Britain and North America.

Only the single original specimen of *Solenochilus springeri* has been recorded from Adair County, Iowa. However, diligent search by Mr. Carlyle B. Campbell of Knoxville, Iowa, has resulted in the procurement of a significant collection of conspecific material from the coal strip-pits in the vicinity of Knoxville, Marion County. These specimens form the main basis of the present study, although one additional representative from the same general area, collected by Mr. Dwayne D. Stone of Marietta College, Ohio, is designated herein as the neotype.

At the time that the collection from the vicinity of Knoxville was being assembled, the specimens were thought to represent a new species. However, Dr. W. M. Furnish and one of us (B.F.G.) studied the material in connection with the preparation of the nautiloid volume of the Treatise on Invertebrate Paleontology (Mollusca 3, Part K; Furnish & Glenister, 1964). They concluded that the specimens from Marion County are conspecific with the orginal type specimen of *Solenochilus springeri* from Adair County.

Systematic Paleontology

Family Solenochilidae Hyatt, 1893
Genus SOLENOCHILUS Meek & Worthen, 1870

Type species: *Nautilus (Cryptoceras) Springeri* White & St. John, 1868, p. 124-125, text-fig. 10; original designation.

Diagnosis.--Loosely coiled, rapidly expanded nautilicones characterized by development of a pair of conspicuous dorsolateral spines at maturity. Mature conch approximating 100 to 200 mm. in diameter, consisting of slightly less than two volutions, and exhibiting a narrowly perforate umbilicus in better

known species. Length of body chamber one-third volution. Shell smooth, growth lines form broad deep hyponomic sinus and shallow narrow dorsolateral sinus. Whorl section strongly depressed (height/width of ½) to equidimensional; dorsum generally flat, but varying from slightly convex to shallowly impressed; greatest width at mid-height in most species but close to umbilical shoulder in others; venter broadly rounded. Pronounced dorsolateral ridge developed progressively on umbilical shoulder of ultimate half volution, expanded into long hollow dorsolateral spine close to mature aperture. Sutures straight to slightly sinuous. Siphuncle ventral, marginal, with diameter 1/10 to 1/20 that of corresponding whorl height. Septal necks straight and almost hemichoanitic on ventral margin, recumbent cyrtochoanitic on dorsal side; siphuncular segments strongly expanded at mid-lenth. Ectosiphuncular sutures delimit characteristic circular area at mid-length of camerae.

Comparison.--The two genera which resemble *Solenochilus* in gross conch form are *Acanthonautilus* Foord 1896, and *Permonautilus* Kruglov 1933.

Acanthonautilus, the only other undoubted representative of the Solenochilidae, is known only from Late Mississippian strata in North America and Europe. It is virtually identical with *Solenochilus* in external morphology, including the form of the dorsolateral spines. However, in those Mississippian solenochilids for which the detailed structures of the siphuncle are known [*e. g. Acanthonautilus collectus* (Meek & Worthen, 1870)], the siphuncular segments are more nearly tubular than in Pennsylvanian representatives of the family. This tubular form of the siphuncular segments is related to the rounded cyrtochoanitic septal necks of the Mississippian species in contrast to the recumbent necks of Pennsylvanian and probably also Early Permian representatives (Furnish & Glenister, 1964, p. K442, fig. 320). More detailed knowledge of the many inadequately documented solenochilid species is necessary before the problems of generic assignment can be resolved. However, present understanding suggests that at least most Mississippian species possess the tubular siphuncle of *Acanthonautilus* whereas Pennsylvanian and Early Permian representatives have expanded siphuncular segments and should be referred to *Solenochilus*.

Permonautilus has been recorded in Late Permian strata from the Russian Platform and the Transcaucasus. Consideration of the affinities of this genus is complicated by the possibility that the syntypes of its type species (*Nautilus cornutus* Golovkinsky, 1868, p. 381-383, pl. 5, figs. 15-19) are not conspecific. However, the general conch form of the largest syntype (Golovkinsky, 1868, pl. 5, fig. 15) is strikingly similar to that of typical *Acan-*

thonautilus and *Solenochilus*. The siphuncle is not visible in the largest syntype of *Permonautilus cornutus*. Other specimens referred to *Permonautilus* possess a subcentral siphuncle, and consequently the genus is referred to the Liroceratidae. Perhaps the resemblances between *Permonautilus* and *Solenochilus* are merely homeomorphic. However, there is a possibility that some of the forms presently referred to *Permonautilus* represent late derivatives of the Solenochilidae in which the siphuncle had migrated from ventral marginal position. A combination of dorsolateral spines, recumbent septal necks and expanded siphuncular segments would necessitate reference to the Solenochilidae. Only detailed study of the siphuncle can clarify the temporal and morphologic relations between *Acanthonautilus*, *Solenochilus*, and *Permonautilus*.

SOLENOCHILUS SPRINGERI (White & St. John, 1868)

Figure 1A,B

Nautilus (Cryptoceras) Springeri WHITE & ST. JOHN, 1868, Trans. Chicago Acad. Sciences, p. 124, fig. 10.

Nautilus (*Solenochilus*) *Springeri* (White & St. John, 1868), MEEK & WORTHEN, 1870, Proc. Acad. Natural Sciences Philadelphia, p. 47-48.

Solenochilus springeri (White & St. John, 1868), MILLER & YOUNGQUIST, 1949, Geol. Soc. America, Mem. 41, p. 131-132, text-fig. 38. FURNISH & GLENISTER, 1964, *in* Treatise on Invert. Paleontology, Part K, Mollusca 3; R. C. Moore, ed., p. K440-442, text-fig. 319,320(1), 321.

Description.--Approximately 10 moderately well-preserved but incomplete specimens of *Solenochilus springeri* and numerous additional fragments from Marion County, Iowa, are available for study. Most comprise the lateral or ventral portions of the last whorl, with some displaying partial or complete spines. Inner volutions of the conch are not generally preserved in the Iowa material. Most specimens have been flattened during diagenesis; however, the spine-like processes show relatively little deformation. A single specimen consists of the ventral and lateral portions of the last whorl, including one spine. This last-mentioned specimen (S.U.I. 11043) is the best representative yet found in Iowa and is hereby designated as the neotype of *S. springeri*, the original type having been lost. Three additional specimens from the Bloyd Formation of northwestern Arkansas complement the Iowa material by exhibiting the details of the phragmocone. In the following discussion, description of the body chamber refers almost exclusively to Iowa material, whereas that of the phragmocone is based on the Arkansas specimens.

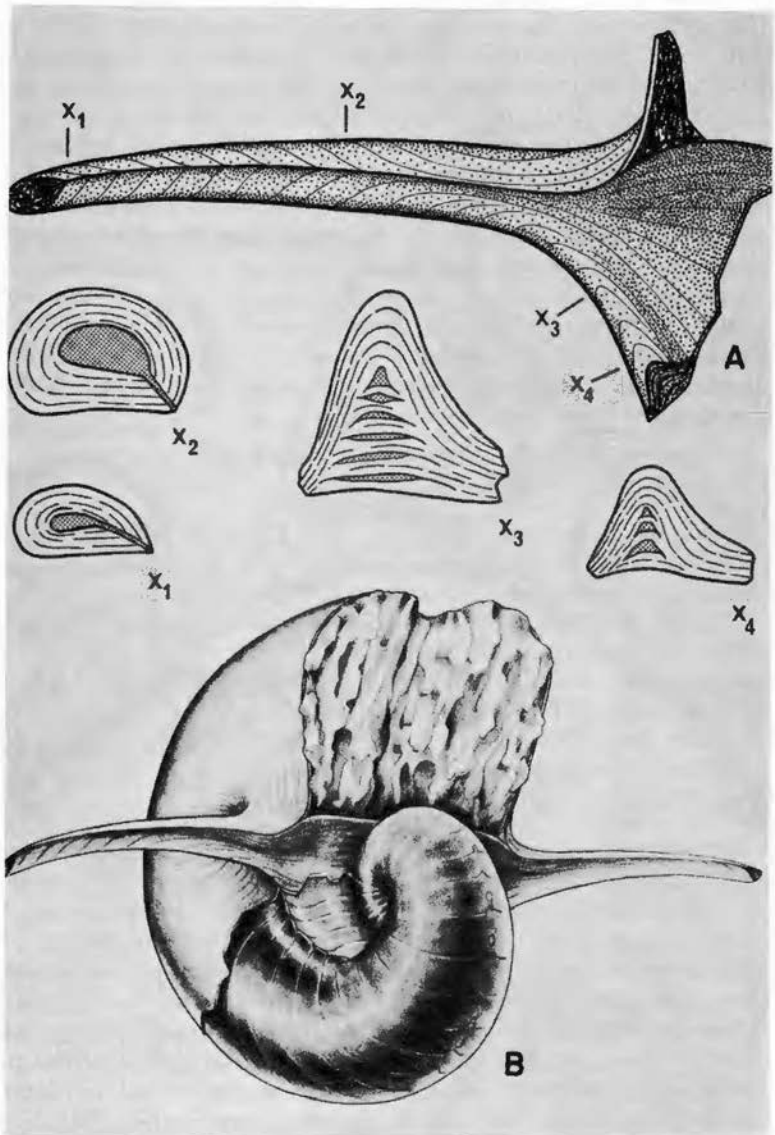

Figure 1. *Solenochilus springeri* (White & St. John)
A. Anterior view of spine and adjacent portions of dorsolateral ridge, and four transverse section (X_1 - X_4) taken along lines indicated; spine natural size, sections twice enlarged; Marion County, Iowa.
B. Obique view, 2/5 natural size; composite, phragmocone based mainly on specimens from Bloyd Formation, Arkansas; spines and body chamber based mainly on material from Marion County, Iowa (from Furnish & Glenister, 1964).

Fully mature conchs achieved diameters ranging from approximately 100 mm. to 150 mm., possibly indicating dimorphism, and consist of one and one-half volutions. The umbilicus is finely perforate, being restricted axially to approximately 3 mm.

Whorls are moderately depressed in all growth stages, the ratio of height/width approximating two-thirds. The whorls are fairly uniformly rounded across the flanks and venter, although somewhat flattened ventrally. Greatest width lies at about mid-height of the whorl. The dorsum is essentially flat, but in the ultimate volution it is bordered by a shallow depression adjacent to the umbilical shoulder. The shell is smooth. Growth lines delimit a deep rounded hyponomic sinus across the entire venter and a corresponding salient on the dorsolateral flanks; a shallow sinus occurs on the flanks adjacent to the dorsolateral ridge, and the ridge is marked by a narrow high salient.

Although somewhat sinuous, the suture is essentially straight. The siphuncle has a diameter approximating 1/10 the corresponding whorl height, and is in contact with the ventral shell wall. Septal necks are straight and long ventrally, where they approximate 2/5 of the septal interval; dorsally they are shorter and recumbent cyrtochoanitic. The connecting ring is strongly expanded behind the tip of the septal neck and tapers gradually to the preceding septal foramen.

In the initial half volution, the umbilical shoulder is uniformly rounded. However, a conspicuous dorsolateral ridge developed progressively on the umbilical shoulder in the ultimate volution, and extended into a long laterally directed spine near the fully mature aperture. Near the base of the spine, the dorsolateral ridge has a maximum shell thickness of approximately 15 mm. Transverse sections of the ridge exhibit clear lamination and reveal the presence of a variable number of completely enclosed elongate cavaties. The number of these cavities increased with progressive development of the ridge, and reached a maximum of ten near the base of the spine. The cavities reflect intervals during which the fold of the mantle beneath the crest of the ridge withdrew inward without correspondingly continuous secretion of shell.

Near the aperture the dorsolateral ridge projects laterally to form the base of the dorsolateral spine. These spines are almost normal to the plane of symmetry of the conch, and lie approximately in the plane of the aperture. They are essentially straight but curve slightly anteriorly. Their length, roughly equal to the width of the mature aperture, is some 90 mm. in large specimens. The posterior surface of the spine is uniformly rounded whereas the anterior margin is angular. The spines are hollow throughout their full length (Figure 1A); a narrow cavity, which housed a projection of the mantle, extends from the body chamber to the tip of the spine. Growth lines indicate that the mantle of the spine was exposed anteriorly during secretion of the basal half of the spine. However, at mid-length the mar-

gins of the upper and lower surfaces of the spine met anteriorly, fully enclosing the axial cavity. Further lateral growth was holoperipheral so that the spine extended as a tube. The line of contact of the dorsal and ventral surfaces of the spine forms a sharply angular seam. No cavities were observed within the shell material of the spine.

Function of the spines remains an enigma. They may have served as hydrodynamic stabilizers, as the transverse section is well streamlined for backward movement. A projection of the mantle must have extended to the tip of the spine, where it could have served a sensory function; a similar function has been postulated for some spinose Jurassic brachiopods (Rudwick, 1965). This same mantle projection would have aided in anchoring the animal in the body chamber.

Periphract scars are visible in the Arkansas specimens, but details of their configuration are not discernible.

Comparison.--Most of the Pennsylvanian species referred to *Solenochilus* are based on such inadequate type material that realistic comparisons are precluded. Many were erected from unique fragments. The internal mold of the holotype of *Solenochilus peculiare* Miller & Owen (1934, p. 254-256, pl. 14, figs. 1,2), from the lower Cherokee Group of Missouri, exhibits a low rounded ventral ridge flanked by a pair of shallow ventrolateral grooves. These peculiarities produce flexures in the suture and may perhaps permit recognition of the species. S. *missouriense* Miller, Lane & Unklesbay (1947, p. 10, pl. 4, figs. 3,4), from the Winterset Limestone of Missouri, has more strongly depressed whorls than type *Solenochilus*; flattening of the ventral whorl section is accompanied by development of a conspicuous ventral lobe. S. *floweri* Gordon (1965, p. 154, pl. 13, figs. 1,2), from the Atoka Formation of Crawford County Arkansas is distinguishable by the subtrapezoidal whorl section of the mature conch. Other described species of *Solenochilus* are too poorly known for adequate specific comparison.

Occurrence.--The only locality given for the original specimen on which *Solenochilus springeri* was erected is "Upper coal measures of Adair County, Iowa" (White & St. John, 1868, p. 125). No additional representatives are known from that area, and all material from Iowa currently available to us was collected from the vicinity of Knoxville, Marion County. The majority of these specimens are from the coal strip-pits now being worked approximately 4 1/2 miles NE of Knoxville (NW1/4 sec. 26, T. 76 N., R. 19 W.). A few additional representatives, including neotype S.U.I. 11043, are from an abandoned coal strip-pit 3 miles NNE of Knoxville (NE1/4 sec. 29, T. 76 N., R. 19 W.). The coal seams in these two strip-pits are probably correlative,

although strata in the vicinity of Knoxville are notoriously discontinuous and difficult to correlate, even over small areas. In each of the strip-pits the coal is some 3 feet thick, and is overlain successively by 10-20 feet of black shale, 1-2 feet of dark grey limestone and an undetermined thickness of black shale. Marine fossils are moderately abundant in the upper 3 feet of black shale beneath the limestone, and occur sporadically in the limestone bed. They include *Solenochilus springeri*, *Pseudorthoceras knoxense* (see Richard Arnold Davis & Carlyle B. Campbell, this volume), abundant acrotretid and strophomenid brachiopods, and gastropods.

The logs of two wells drilled in the area between our two Marion County *Solenochilus* localities were made available through the courtesy of Orville J. Van Eck, Iowa Geological Survey. Study of these wells suggests that the coal beneath our fossiliferous horizon lies approximately 100-150 feet above the Mississippian-Pennsylvanian unconformity. The entire Pennsylvanian section in the wells lies within the Cherokee Group, and almost certainly belongs in the lower Cherokee. Our fossiliferous horizon is probably Desmoinesian, but we are unable to preclude the possibility of an Atokan assignment.

Three specimens of *Solenochilus springeri* from Arkansas have been utilized in determining the form of the phragmocone. S.U.I. 12543 and 12544 are from the Trace Creek Shale Member of the Bloyd Formation (Morrowan), Washington County, where they were found in association with *Diaboloceras neumeieri* Quinn & Carr (1963). They were collected during 1961 by James A. McCaleb and W. M. Furnish. The remaining specimen is in the University of Arkansas collections and was secured by Tom Vest from the Dye Shale Member of the Bloyd Formation (Morrowan), Cleburne County.

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