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THE MIXOCHOANITIC CEPHALOPODS

by

A. K. MILLER

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The writer wishes to acknowledge his indebtedness to Professor C. O. Dunbar of Yale University for advice in this study. Acknowledgment is due also to the recent work of Dr. August F. Foerste on nautiloid cephalopods, which has led to a far better understanding of that group than was ever achieved in the past.

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INTRODUCTION

The classification of the nautiloid cephalopods is not in as satisfactory condition as is that of most of the other major groups of fossil invertebrates. The earlier paleontologists attributed great importance to the external form of the shell, and they distinguished such groups as *longicones* and *brevicones*, and such genera as *Orthoceras, Cyrtoceras, Gyroceras, Gomphoceras, Trochoceras, Lituites,* etc.—all based on the shape of the conch. Barrande recognized that the structure of the siphuncle, the shape of the aperture, etc. were significant, but he considered them as subordinate in importance to the general form of the conch. Zittel followed Barrande, and it remained for Hyatt to establish a genetic classification and emphasize that "the general form and involution of the shell" are "relatively minor characters" and that surer guides to the affinities of the species and genera are to be found in "coincidence of structure, outlines of the aperture, and especially resemblances in developmental stages."

In the Zittel-Eastman *Text-book Palaeontology* (1900) Hyatt introduced a scheme of classification which followed the general principles outlined in his previous scheme (*Genera of Fossil Cephalopods,* 1883) but contained important modifications. A note by the translator in this volume (p. 592) tells us that "the classification and diagnoses are condensed from an exhaustive Monograph on fossil Cephalopods, at present still in MS., which embodies the results of his [Hyatt's] life-study." Unfortunately, owing to Hyatt's untimely death, this monograph was never completed, and we must regard the published classification as a tenative one in which the major features of Hyatt's philosophy are outlined, but in which the details are still to be worked out. As such it has much to commend it in comparison to any of the other classifications that have appeared before or since the time of its publication, and it clearly demonstrates that Hyatt's grasp of the group as a whole was far superior to that of any of his predecessors or successors.

In America Hyatt's classification has been accepted ever since its appearance in 1900, but most European paleontologists failed to recognize the value of this genetic classification and continued to adhere to the old artificial one. However, two of the outstanding Swedish students of nautiloids, Holm and Troedsson, accepted Hyatt's work with comparatively few reservations, and from the recent writings of Pompeckj, Schindewolf, and Teichert and the last editions of Zittel's *Grundzüge der Paläontologie* we see that the Germans also are regarding it favorably. Abel, however, concludes that Hyatt's scheme is only provisional and has recently accepted the classification of the paleobiologist Dacqué, which is based chiefly on the morphological features of the siphuncle.

On the basis of the construction of the siphuncle and related structures, features which are more resistant to adaptation than is the external form of the shell, Hyatt (somewhat as Saemann had done as early as 1854) divided the nautiloids into several major groups, which he subdivided according to the form of the conch, nature of the surface sculpture, shape of the septa, etc. Several of these groups have recently been studied in detail by Foerste, and it is the purpose of this paper to consider another, the Mixochoanites. This study was undertaken when during work on related forms the need for certain changes in nomenclature and arrangement of genera and families in this group became apparent.

PREVIOUS VIEWS IN REGARD TO THE CLASSIFICATION OF THE MIXOCHOANITES

The affinities of the little group of aberrant forms to which Hyatt eventually gave the name "Mixochoanites" have been a puzzle ever since their discovery by Barrande, who originally characterized them as being "très-bissares." He knew only a very few representatives, but he placed them in two or three genera and regarded them as constituting a family of equivalent rank with that which contained all the rest of the multitudinous nautiloids. He was followed in this by P. Fischer, but Zittel, Foord, Billings, Blake, Giebel, Wiltshire, and Wright apparently considered these forms much less distinct, and because of their short, stout living chambers placed them in the immediate vicinity of the gomphoceratoids. Koken placed them between the Orthoceratidae, in which he included *Gomphoceras, Endoceras,* and *Orthoceras,* and the Cyrtoceratidae, in which he included *Cyrtoceras* and *Phragmoceras.* Eichwald regarded *Ascoceras* as closely related to *Nothoceras* and the living *Sepia*; Roemer, however, placed it next to *Trochoceras*; Bronn and Woodward next to *Gyroceras*; Philippi between *Lituites* and *Cyrtoceras*; and Nicholson in his sub-family Orthoceratidae. Lindström, who apparently studied the group in more detail than any of the other paleontologists except perhaps its discoverer, regarded it as related to the forms referred to *Cyrtoceras* by Barrande and to the poterioceratoids.

Hyatt in his *Genera of Fossil Cephalopods*, 1883, added genera hitherto not considered related to the group, and divided it into two families, the Mesoceratidae and the Ascoceratidae; *Mesoceras* Barrande and a then new genus *Billingsites* constituted the first, and *Aphragmites, Ascoceras, Glossoceras,* and *Ophidioceras,* all of Barrande, the second. These two families were placed between the Gomphoceratidae and the Maelonoceratidae in the suborder Ellipochoanoida, which included most of the nautiloids known at that time. However, in discussing the Mesoceratidae, Hyatt (p. 278) stated that they are "very distinct as a group from all other forms except the Ascoceratidae."

When he revised this classification in 1900, he emphasized this former opinion by placing these two families in a separate suborder, parently uncrushed specimens (internal molds) the aperture appears to have been entirely closed led Karpinsky to the conclusion that the adoral part of the conch was soft and flexible whereas the rest was rigid. Schindewolf has discussed the composition of the shell at some length and has ably presented the available evidence for believing that the shell was calcareous rather than chitinous.

The relationship of this Lower Cambrian genus to the later cephalopods has recently become a moot question, and at present there is little agreement of opinion as to its proper place in our scheme of classification of the invertebrates. In 1900 Hyatt disregarded the prevalent opinion that its affinities were with the Orthoceratidae and placed it in the Ascoceratidae next to *Glossoceras,* apparently only because Schmidt's figures led him to the erroneous conclusion that its living chamber is "flaring and uncontracted" and because its septa are superficially similar to those of *Choanoceras.* It is now known that all but the extreme adapertural part of the living chamber is expanded adorally at the same rate as the phragmacone, and the aperture is greatly restricted; therefore, as recent authors have unanimously agreed, there seems to be no justification whatever for leaving this genus in the Mixochoanites.

Grabau and Shimer in 1910 created the suborder Protochoanites for the reception of this Cambrian genus, and in 1919 the senior of those two authors suggested that it was "ancestral, on the one hand, to the Holochoanites, and on the other to the Orthochoanites. By a crowding of the septa the endocones of the so-called siphuncle of the Holochoanites is produced, while a shallowing and separation of the septa produces the septa of the Orthochoanites. The septa chambers of the Holochoanites are a new feature. The endocones of the Holochoanites are considered the homologues of the septa of the Orthochoanites. On this view, the 'siphuncle' of the Holochoanites is the homologue of the entire Orthocern shell, while the endosiphuncle is the homologue of the Orthoceran siphuncle, and the endosipholining, when present, the homologue of the Orthocern shell proper."

Grabau has since (1922) reiterated these views, amplified his discussion of them, and added (p. 62) that the "*Cyrtochoanites* . . . may have been derived from primitive *Orthochoanites,* or they may represent an independent line of evolution from the ancestral stock . . ., the former view the more likely one." [a]

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[a] Since these statements were written, a still later discussion of this subject by

Similar conclusions were reached apparently independently by Dacqué in 1921, but he places *Volborthella* and *Orthoceras* in the same group, believing that the only distinction between them lies in the composition of the conch, probably conchyolin in the former but calcium carbonate in the latter; and he regards the large actinoceratoid siphuncle as well as that of the endoceratoids as the homologue of the conch of *Volborthella, Orthoceras, Cyrtoceras,* and *Nautilus.* He also postulates that whereas most of the later coiled nautiloids developed directly from *Volborthella* through *Orthoceras,* part of them have evolved from the endoceratoids by a reduction of the size of the siphuncle.

Abel has considered these views favorably, but Schuchert, Clarke, and Ulrich[1] questioned the validity of the homologies suggested by Grabau immediately after their postulation. Troedsson (pp. 16-20) has shown reasons for believing that *Volborthella* is not the direct progenitor of *Orthoceras* and that the siphuncle of *Orthoceras* is not homologically different from that of *Endoceras,* but he has accepted the conclusion that the conch of *Volborthella* is homologous with the siphuncle of the endoceratoids. Schindewolf (pp. 74-77) on the contrary regards *Volborthella* as a typical representative of the Orthochoanites, and has demonstrated that its conch as well as those of the later Orthochoanites is to be homologized with the entire conch of the endoceratoids and not with the siphuncle alone.

Foerste (1925, p. 4) has stated that "*Volborthella* has no relationship to this group [the Mixochoanites], but should be associated with *Salterella.*" Schindewolf interpreted this statement as meaning that Foerste believes *Volborthella* not to be a cephalopod, as do Krause and Gürich[2]. Foerste in all probability holds that opinion, but in 1924 Thomas Clark referred *Salterella* to the family Orthoceratidae and briefly presented his reasons for doing so, and more recently (1927) Poulsen, while studying forms from

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Grabau (Bull. Geol. Soc. China, vol. 8, 1929, pp. 115-123) has come to the writer's attention. In it Grabau modifies his earlier conclusions in that both *Volborthella* and *Salterella* are regarded as primitive orthochoanites but are not believed to be ancestral to the holochoanites, which are stated to have arisen from *Teilhardoceras,* a hypothetical "genus." However, Grabau concludes this discussion with the following sentence: "These statements [presumably the whole paper], however, must be taken as mere suggestions and guides to future study which may or may not substantiate their validity."

[1] See "Discussion" following Grabau's paper of 1919.

[2] See "Diskussion" following Schindewolf's paper of 1928.

the Lower Cambrian of northwestern Greenland and comparing them with American specimens, has concluded that *Salterella's* "cephalopod characters are very conspicuous." Clark's discussion is supplemented by a number of pen sketches that bear a striking resemblance to undoubted cephalopods, and he claims to have observed "siphonal collars" and a central aperture in each septum "from which a siphuncle-like tube projects backward to the next posterior septum." Specimens in the paleontological collections of Peabody Museum, Yale University, fail to show such structures, but in fairness it should be emphasized that they came from a different locality than those figured by Clark; however, Poulsen also was unable to observe "siphonal collars" and he states that "the shell of this genus differs from that of the later Nautiloidea in its structure."

It should also be mentioned in this connection that Walcott has recently (1913) described as "*Cyrtoceras cambria*" minute curved conical fossils from the Upper Cambrian of China that appear to possess saucer-shaped septa and a small marginal siphuncle, the structure of which, unfortunately, was not investigated. These fossils undoubtedly represent a new and distinct genus, and the published figures of them certainly bear out their postulated cephalopod affinity. However, it will be well to reserve judgment as to their significance and relationships until the structure of their siphuncle has been investigated and they have been studied by more than one observer. It should perhaps be mentioned that Kobayashi (1931) has recently suggested that "*Cyrtoceras cambrica* . . . may possibly be an Ellesmereoceroid, as judged from its description and illustrations," whereas Schindewolf (1928, p. 81) is inclined to regard it as a cyrtochoanite and points out that its narrow siphuncle indicates that it is not a holochoanite.

With the exception of this single minute form, which is imperfectly known, even questionable cephalopod remains appear to be entirely absent from all of the Middle Cambrian (except possibly its very base) and all of the Upper Cambrian [2a] (Ozarkian excluded); and Foerste (1925, p. 14) has recently shown that all of the Ozarkian and Canadian cephalopods are holochoanites. Those who postulate that either or both of the Lower Cambrian

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[2a] Grabau (Bull. Geol. Soc. China, vol. 8, 1929, p. 122) has recently stated that orthoceracones and cyrtoceracones which appear to have orthochoanitic siphuncles occur in the "uppermost Cambrian beds" of Shantung. However, no description or illustration of these forms has so far been published.

forms, *Volborthella* and *Salterella*, are cephalopods are almost unanimous in the conclusion that they are orthochoanites; therefore, if we are to regard them as ancestral to the later cephalopods, we must postulate that orthochoanites, which for some unexplained reason failed to leave a record in Middle and Upper Cambrian times, evolved into holochoanites, which, in turn, later gave rise to orthochoanites; or that orthochoanites actually existed during Middle Cambrian, Upper Cambrian, Ozarkian, and Canadian times, but we have failed to discover a trace of them as yet. Both of these possibilities are extremely improbable, and it now seems to the writer that we should regard *Volborthella* and *Salterella*, which apparently should be associated in our classification, as pteropods, conulariads, or foraminifers, i.e., not cephalopods; or, if they are cephalopods, we should consider them as representing an aberrant side-branch which learned to secrete "hard-parts" early in Cambrian times but died out[3] before or shortly after the beginning of the Middle Cambrian, whereas the forms that were ancestral to the rest of the cephalopods remained naked and therefore recordless until Ozarkian times.

Genus OPHIOCERAS Barrande 1865

[= *Ophidioceras* Barrande 1867, but not *Ophioceras* Hyatt 1867]

Plate II, Figs. 1, 2

The generic term "*Ophioceras*" was originally introduced[4] in 1865 by Barrande in a volume of plates (explanation of plate 45) as a subgenus of *Lituites* to include the forms in which the free straight anterior portion of the conch is short and the aperture contracted, or, to be exact, "pour les formes à crosse courte et à ouverture contractée, qui caractérisent la faune troisième silurienne et qui contrastent avec les *Lituites* à longue crosse et à ouverture non contractée? de la faune seconde." The text to accompany these plates did not appear until two years later, and in it Barrande (p. 174) transformed his term *Ophioceras* to *Ophidioceras*, stating that he did so to avoid confusion with

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[3] The specimens from the Stones River of Tennessee that were briefly described by Safford (Geology of Tennessee, p. 289, Nashville, 1869) as "*Salterella Billingsi*" need to be restudied, but there seems to be little justification for their reference to the Lower Cambrian genus *Salterella*.

[4] "*Ophioceras*" *simplex* was figured by Barrande as early as 1855 (Bull. Soc. géol. France, 2e sér., t. 12, pl. 5, fig. 6) but was referred to *Lituites*.

Ophiceras[5], which was applied by Suess[6] to a group of ammonites during the printing of the plates and before their publication. According to the International Rules of Zoological Nomenclature (Recommendations following Article 36) *Ophioceras* is not to be rejected as a homonym of *Ophiceras;* therefore Barrande's earlier term, having priority, must be regarded as the valid name of the genus.

In 1867 Hyatt[7], without taking into consideration Barrande's earlier use of the term, employed *Ophioceras* for a then new genus of ammonites. Later, in 1900 (p. 575) he listed this genus as a synonym of one of his later genera *Caloceras*[8] Hyatt 1871, apparently rejecting his earlier term as a synonym of *Ophioceras* Barrande 1865, but not stating so. Nevertheless, *Ophioceras* Hyatt was inadvertently resurrected in the second edition of the Zittel-Eastman *Text-book of Paleontology* (p. 655) by J. P. Smith and *Caloceras* was dropped. Broili (1924, pp. 571, 572) places these two genera in different subfamilies, but as far as the writer has been able to learn, they are synonyms and *Caloceras* is in good standing whereas *Ophioceras* Hyatt is to be rejected as a homonym of *Ophioceras* Barrande.

Barrande did not designate a type for his subgenus *Ophioceras* [*Ophidioceras*], and recently Foerste (1930, p. 19) has selected "*Ophidioceras simplex* Barrande" as such. However, as early as 1868, Tate[9] listed *Lituites nakholmensis* Kjerulf of the Ordovician of Nakholmen, Norway, as the genotype, and this designation is

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[5] This term is now generally ascribed to Greisbach, who however did not use it until 1880 (Records of the Geol. Survey of India, vol. 13, p. 109). Since it was preoccupied, a new generic term is needed for Greisbach's genus, and it is here proposed to call it *Greisbachoceras*, in honor of its original describer. The type of this genus is *Greisbachoceras* [*Ophiceras*] *tibeticum* (Greisbach) of the Lower Triassic of the Himalayas, and the generic characters are ably set forth by Greisbach (op. cit.), Hyatt and Smith (U. S. Geol. Survey Professional Paper 40, pp. 117-118, 1905), and Krafft and Diener (India Geol. Survey Mem., ser. 15, vol. 6, mem. 1, pp. 80-81, 1909).

[6] Suess, Eduard, Anzeiger der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe, II. Jahrgang, p. 112, 1865.

[7] Hyatt, Alpheus, The fossil cephalopods of the Museum of Comparative Zoölogy: Harvard Coll. Mus. Comp. Zoöl. Bull., vol. 1, p. 75, 1867.

[8] Proposed in a footnote by Alpheus Hyatt (On reversions among the ammonites: Boston Soc. Nat. Hist. Proc., vol. 14, p. 29, 1871), and later treated of at length by the same author (Genesis of the Arietidae: Memoires Museum of Comparative Zoölogy at Harvard College, vol. 16, no. 3, pp. 136-154, 1889).

[9] Tate, Ralph, Appendix to the Manual of Mollusca . . . by S. P. Woodward, 2d ed., p. 8, London, 1868.

"not subject to change." This latter species is not very similar to the forms figured and described by Barrande, which came from the Middle Silurien of Bohemia, and as it is rather deeply involute, though becoming less so near the aperture, and does not possess a free straight extension of the living chamber, it is not congeneric with them. Nevertheless, it was considered so by Barrande, and although the designation of it as the genotype seems very inappropriate, it is "not subject to change."

Kjerulf[10] figured this species and listed the general horizon and locality from which the type came, but he did not describe it. No other forms are known to the writer that are congeneric with this species, and a generic diagnosis is not attempted here as neither specimens nor description is available for study; Kjerulf's figures, however, are reproduced.

In his *Genera of Fossil Cephalopods*, 1883 (p. 279), Hyatt placed *Ophidioceras* Barrande [=*Ophioceras* Barrande] in the family Ascoceratidae, and stated: "The costated, compressed whorls have some resemblance to those of Ascoceras and the aperture is closely similar to Glossoceras. . . . We place them [the *Ophidioceras* shells] provisionally near Ascoceras on account of the Y shaped apertures and form of whorl and costations." However, by 1893, Hyatt had become aware of the incorrectness of this reference, and he (p. 513) removed the genus in question from the Ascoceratidae and made it the type of a new family, which in 1900 (p. 520) he placed in a different suborder from that to which he referred *Ascoceras* and its allies. This latter classification is by far the more tenable, and it will suffice here to state that none of the forms that have been referred to "*Ophidioceras*" appears to be at all closely related to any of the mixochoanitic nautiloids.

Genus EUOPHIOCERAS Miller, n. gen.

Plate II, Figs. 3-7

As noted above Barrande established the genus *Ophioceras* [=*Ophidioceras*] for a group of Silurian forms from Bohemia but included an Ordovician form from Norway, apparently only because of a superficial resemblance of the aperture. Unfortunately, this Ordovician form was later chosen as the genotype, and as

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[10] Kjerulf, Theodor, Veiviser ved Geologiske Excursioner i Christiania Omegn, . . ., p. 9, text fig. 21, p. 13, Christiania, 1865.

it is not congeneric with the Silurian ones, a new generic name is needed for the latter. In as much as the genus was actually established for the Silurian forms, the term *Euophioceras* is here proposed for them, and *Lituites* [*Ophioceras, Ophidioceras*] *simplex* Barrande of Stage E of the Middle Silurian of Bohemia is designated as the genotype.

The characters of this genus are admirably set forth by Barrande (pp. 174-176), and the reader is referred to his voluminous monograph for a detailed generic diagnosis; also a concise diagnosis has recently been published by Foerste (1930, pp. 19-20). The following species should be referred to this genus: *Ophidioceras* [*Ophioceras*] *amissus* Barrande, *O. proximus* Barrande, *O. rudens* Barrande, *O. simplex* (Barrande), *O. tener* Barrande, *O. tesselatus* Barrande, all of Stage E of the Silurian of Bohemia; *O. reticulatum* Angelin and *O. rota* Lindström of the Middle Silurian of Gotland; *Lituites articulatus* Sowerby[11] and *Ophidioceras geometricum* Blake of the Silurian of England; *Ophidioceras wilmingtonense* Foerste of the Cedarville dolomite of Ohio and the Racine dolomite of Wisconsin; *O. welleri* Foerste of the Racine of Illinois; and probably the specimen from the Silurian of Cornwallis Island, Arctic America, that was described by Salter[12] as "Lituites ——, n. sp."

Barrande (vol. 2, texte 4, p. 510) included *Lituites nakholmensis* Kjerulf of the Ordovician of Nakholmen, Norway, and *Clymenia depressa* (Eichwald) 1860 [= *Nautilus depressus* Eichwald 1840] of the Middle Ordovician of Odinsholm, Estonia, in the same genus as all of the above listed forms known at that time, but the internal molds of both of those species are smooth and the adoral part of their conchs is in contact with the preceding volution. It is true that the degree of involution in both species decreases adorally and "*Nautilus*" *depressus* may belong in the same family as *Euophioceras*, but the general shape of the conch and the nature of the sutures of *Lituites* [*Ophioceras*] *nakholmensis* is so different from that of the species here referred to

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[11] Sowerby, James de C., in Murchison, R. I., The Silurian System . . ., part 2, p. 622, pl. 11, fig. 5 [but not fig. 7, the original of which was later described as "*Cyrtoceras extricatum*" by Blake (A monograph of the British fossil Cephalopoda, pt. 1, pp. 183-184, 1882)], London, 1839.

[12] Salter, J. W., Geology; Appendix in Sutherland, Peter C., Journal of a voyage in Baffin's Bay and Barrow Straits . . ., vol. 2, p. ccxxii, London, 1852.

Euophioceras, that it seems very doubtful if they are at all closely related.

To avoid ambiguity, it should perhaps be repeated here that none of the above listed forms is at all closely related to any of the mixochoanitic cephalopods, and *Euophioceras* should be associated with *Lituites* and not the ascoceratoids.

Genus MESOCERAS Barrande 1877

Plate II, Figs. 8-12

This genus was established by Barrande in 1877 (pp. 198-200) on a single internal mold of a living chamber from Stage E of the Middle Silurian of Bohemia. Barrande states that he kept the specimen for twenty-five years before describing it, waiting in vain for the discovery of other specimens that would elucidate more of the specific and generic characters, and since that time no other representative of the genus has been found.

The holotype of the only known species, *Mesoceras bohemicum* Barrande, appears to represent a short, stout brevicone, that is elliptical in cross section as it is slightly depressed dorso-ventrally. The living chamber is very short and the aperture is greatly restricted dorsally and somewhat so ventrally, but not at all laterally. It is narrowly elliptical in outline, but there appears to be a small hyponomic sinus on the ventral side. Barrande states that as the specimen is preserved in black slate he was not able to determine definitely whether the ventral notch was original or was due to an accident during preservation, but the growth lines bend adapically as they cross an indistinct longitudinal median groove on the ventral side of the conch and therefore indicate that the notch represents a hyponomic sinus. The sutures are simple and straight and are directly transverse to the long axis of the conch. The siphuncle is central in position and is relatively small at its passage through a septum, but the shape of its segments and its general nature are not known; nor is anything known as to the nature of the phragmacone.

Barrande was unable to place this genus satisfactorily in his classification, for he divided the nautiloids into two major groups on the basis of the nature of the aperture, and he considered that of *Mesoceras* as neither simple nor composite. Hyatt in 1883 (p. 278) made this genus the type of a new family and associated his own then new genus *Billingsites* with it, apparently only because both were brevicones with short, bulbous living chambers and restricted apertures. He placed this family between the Gomphoceratidae and the Ascoceratidae but stated that the members of it were "very distinct as a group from all forms except the Ascoceratidae." Later, in 1900 (pp. 515-516) he combined this family with the Ascoceratidae to form a new suborder, the Mixochoanites. Zittel and Broili followed Hyatt in part and left *Mesoceras* associated with *Billingsites*, but Fischer, Foord, and Lindström placed it with the gomphoceratoids. This latter classification seems logical to the writer, but until the nature of the siphuncle is established, it will not be possible to classify the genus with certainty. However, it does not appear to be at all closely related to any of the true Mixochoanites, i.e., *Ascoceras* and its allies, and there seems to be no justification for leaving it in that suborder.

Genus PROBILLINGSITES Foerste 1928

Plate III, Figs. 10-13

Foerste (1928, pp. 317-320) has recently recognized that four of the species previously referred to *Billingsites* are distinctly more primitive than typical representatives of that genus and has proposed the generic term *Probillingsites* for them. Unfortunately, each of these species is based on a single fragmentary specimen, the earlier stages of the conch are not known, and the siphuncle has not been observed. Nevertheless, it seems clear that this group is distinctly intermediate between *Billingsites* and its progenitor, an *Oncoceras*-like form, and it should be regarded as the most primitive member of the Mixochoanites.

The genus includes *Probillingsites welleri* Foerste probably from the Galena of Wisconsin, *P. williamsportensis* (Foerste) from the Catheys formation of western Tennessee, *P. primus* (Fritz)[13] of the Upper Cobourg member of the Utica group of southern Ontario, and *P. manitoulinensis* (Foerste) from the Meaford member of the lower Richmond of Manitoulin Island. The last species listed is of Upper Ordovician age and the two preceding ones are of Middle Ordovician; the horizon of the other species, the genotype, is uncertain, but there is good reason to believe that it also is Middle Ordovician in age. The genus then appears to be characteristic of the Middle Ordovician but to have

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[13] Described in Parks, W. A., Faunas and stratigraphy of the Ordovician black shales and related rocks in southern Ontario: Royal Soc. Canada Trans., 3d ser., vol. 22, pp. 85-86, 1928.

continued on into the Upper Ordovician, where its place is largely taken by *Billingsites* and *Schuchertoceras,* discussed below.

The conch is breviconic and moderately small, and in complete specimens would probably be similar in shape to that of *Oncoceras,* but only the adoral obese, ovoid expansion is known. This consists of the living chamber and the two to four adoral camerae. It is typically depressed dorso-ventrally, but in *P. manitoulinensis,* the last representative of the genus known, it is slightly compressed laterally. The dorsum is straight or slightly concave or convex, but the venter is invariably strongly convex, with the result that the specimens appear very obese. The maximum transverse dimensions of this ovoid expansion are attained near its mid-length, and the conch contracts both adapically and adorally from that point. There is a short indistinct neck-like extension of the living chamber next to the aperture, called the "neck" by Foerste, but the exact nature of the aperture has not been determined. The adoral septa, the only ones known, are not transverse to the long axis of the conch, as are those of most nautiloids, but are strongly inclined to it, and along the lateral sides of the conch the sutures slope strongly adorally from the venter and cross the dorsum as broad rounded saddles; the dorsal part of the living chamber is therefore very much shorter than the obese ventral part. The sutures are slightly sigmoidal, but there is no strong reversal in their curvature, and the dorsal saddles of the adoral septa do not extend as far orad as they do in *Billingsites.*

The sutures of *P. primus* and *P. manitoulinensis* are distinctly intermediate between those of *P. williamsportensis* and *P. welleri* and those of *Billingsites*; they are more closely crowded than those of the last two mentioned species, more strongly inclined to the long axis of the conch, and more strongly sigmoidal, and at least two of them appear to coalesce along the lateral sides of the conch. Also the conchs of both of these species are distinctly concave along the dorsum near the junction of the phragmacone and the living chamber, and the adoral neck-like extension of the living chamber is longer and much more distinct than it is in the other two representatives of the genus. In view of these differences, and since these two species occur in a higher horizon than does the genotype and *P. williamsportensis,* it may eventually prove desirable to recognize them as representing a distinct genus intermediate between *Probillingsites* and *Billingsites*, but at present such a generic refinement seems unnecessary.

Most of the paleontologists who have studied *Ascoceras* and its allies have agreed that the conch was truncated during the life of the individual, i.e., the earlier stages of the phragmacone were broken off along a septum and abandoned after maturity was reached. This inference is based largely on the fact that with very few exceptions only the extreme adoral part of the phragmacone has been found attached to the living chamber—the genus *Ascoceras* was known for a decade before the younger stages of the phragmacone were discovered. Similarly, trucation can be inferred in *Probillingsites*, the earliest and most primitive member of the group known, for none of the described representatives of the genus retains the adapical part of the phragmacone, and all appear to have been bounded adapically by a moderately large, well developed septum, the septum of truncation.

Genus SHAMATTAWACERAS Foerste and Savage 1927

Plate III, Figs. 1-3

Very little information is available in regard to the genus *Shamattawaceras*, for it is based on a single rather poorly preserved, fragmentary specimen. Externally, at least, it is very similar to *Probillingsites*, and in view of no evidence to the contrary, it should be associated tentatively with that genus in our scheme or classification and accordingly referred to the Mixochoanites.

The holotype of *Shamattawaceras ascoceroides* Foerste and Savage, the only known representative of the genus, came from the Shamattawa limestone (Richmond) of northeastern Manitoba, southwest of Hudson Bay. It is an internal mold representing much of the living chamber and the adoral three camerae, i.e., the adoral obese portion of the conch. It is not complete aperturally, and it is bounded adapically by the impression of a large well developed septum; the earlier stages of the phragmacone may have been truncated during the life of the individual as they were in most of the Mixochoanites.

The known portion of the conch is almost semicylindrical in shape but is slightly curved lengthwise; it is almost semicircular in cross section as it is greatly flattened ventrally, narrowly rounded ventro-laterally, and evenly rounded dorso-laterally and dorsally. The venter is convex lengthwise, and the dorsum appears to be slightly so. The adapical part of the holotype is expanded orad very gradually, but the rate decreases adorally and the adoral part of the specimen, which does not represent the aperture is neither contracted nor expanded in a lateral direction. The maximum dorso-ventral diameter of the conch apparently is attained near the mid-length of the specimen, and it decreases both apicad and orad of that point. The specimen is bounded adapically by the impression of a septum which was only very slightly convex apicad in a lateral direction but rather strongly so in a dorso-ventral direction as its dorsal half was curved strongly orad. Since the lateral and apical sides of the specimen are only very slightly convex, it appears subquadrate when viewed from above or below, i.e., in dorsal or ventral aspect, and it would appear so in longitudinal section. Unfortunately, nothing is known as to the nature of the adoral part of the living chamber or the aperture.

On the flat ventral side of the holotype all four of the sutures are parallel and very close together, and they are almost transverse to the long axis of the conch but curve very slightly apicad and therefore form very broad shallow ventral lobes. Along the lateral sides of the specimen they diverge gradually and curve orad at successively greater angles. They form broad, deep rounded saddles as they cross the dorsum, and the dorsal part of the living chamber is therefore very much shorter than the ventral part. Nothing is known in regard to the siphuncle of this genus as no trace of it remains in the only representative that has so far been found.

Although many of the most significant of the generic characters of this form are not known, e.g., the adoral and adapical portions of the conch, the siphuncle, and the aperture, the general shape of the preserved part of the conch and the nature of the sutures indicate a relationship with *Probillingsites*, and in view of complete lack of evidence to the contrary, this genus, for the present, at least, should be associated with *Probillingsites* and placed in the Mixochoanites. As far as is known at present, it differs from *Probillingsites* chiefly in the shape of the adoral obese expansion of the conch; that of *Probillingsites* is subovoid in form and broadly elliptical in cross section, whereas that of the genus under consideration is almost semicylindrical in shape and semicircular in cross section. Occurring as it does in the Richmond, this genus may have developed out of *Probillingsites* or its progenitor, or it may represent a parallel development of an unrelated stock; the nature of the siphuncle and the aperture, when fully known, will doubtlessly remove this uncertainty and enable us to classify the genus definitely.

GENUS BILLINGSITES Hyatt 1883

Plate IV, Figs. 1-6

Ascoceras-like forms were reported from the Ordovician (English Head of Anticosti Island) as early as 1857 by Billings, but it was not recognized that they were generically distinct from typical *Ascoceras* until 1883[14]. In that year Hyatt (p. 278) proposed the generic term *Billingsites* (inadvertently written "Billingoceras", p. 279) for them, designated *Ascoceras canadense* Billings as the type, and defined the genus as including "Silurian species having stout cones, almost globular on account of their truncation and which have dumb-bell shaped apertures, without ventral sinuses." Later, in 1900 (p. 516) he redefined the genus as follows: "Aperture without hyponomic sinus. Gerontic living chamber partly filled by dorsal sigmoidal saddles as in *Ascoceras*, but septa complete on ventral side. Silurian."

Neither of these definitions is very lucid and both are erroneous, for no known representative of the genus possesses a dumb-bell shaped aperture, and the latter definition implies that the septa are not complete on the ventral side of *Ascoceras*, a view held by Barrande but previously recognized by Hyatt (1883, pp. 278-279) as incorrect. Therefore, the genus, though recognized by Zittel and Bassler, was almost entirely neglected until 1924, when it was revived by Foerste and placed on a firm basis. Since that time it has been recognized by various authors, and a considerable number of species has been referred to it.

The type species, *Billingsites* [*Ascoceras*] *canadensis* (Billings) of the English Head and Vauréal (Richmond) of Anticosti Island has recently been studied by Foerste, and the holotype has been redescribed and figured. It should be emphasized that only the adoral obese, ovoid expansion of the conch is known; the earlier stages of the phragmacone apparently were truncated during the

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[14] As early as 1867, Barrande (p. 353) stated that "*Ascoceras*" *deforme* Eichwald of the Upper Ordovician (or Lower Silurian) of Estonia "n'est pas un *Ascoceras*" but reminds of *Gomphoceras;* this conclusion, however, was reached largely because of the inadequacy of Eichwald's figure and description.

life of the individual, and all the knowledge we have of them in this genus is inferred from the scar or cicatrix of attachment.

The known portion of the conch of the genotype, the adoral ovoid expansion, consists of the living chamber and the adoral three camerae. It is subovate in shape, narrowly rounded apicad, and somewhat contracted orad; its maximum transverse dimensions are attained near its mid-length, and it is elliptical in cross section as it is slightly depressed dorso-ventrally. The adoral end of the living chamber is projected into a short indistinct neck-like extension which is contracted orad only very slightly, and the aperture is broadly elliptical in outline. Nothing is known in regard to the exterior of the shell of this species[15], but the internal mold is smooth, with the exception of a broad, shallow, indistinct transverse constriction on the apical fourth of the specimens.

The impression of the septum of truncation on the internal mold shows that it is moderately convex apicad, circular (or nearly so) in outline, asymmetrically subconical in shape, and strongly oblique to the long axis of the conch; it slopes orad from the venter. The suture of the next septum is essentially parallel and almost in contact with the septum of truncation along the ventral and lateral sides of the conch, but along the dorso-lateral sides it curves abruptly ventrad and orad and continues in that direction to the middle of the lateral sides of the conch, where it gradually ceases to swing ventrad and then curves rather abruptly dorsad and continues across the dorso-lateral and dorsal sides of the conch as an essentially straight line transverse to the long axis of the conch. The next septum is almost parallel to the preceding one; along the venter these two septa are about 2 mm. apart, but they gradually converge dorsally, and on the dorso-lateral sides of the conch, where the strong reversal in their curvature occurs, they are only a little more than ½ mm. apart. Orad of this point they gradually diverge so that they are some 9 mm. apart along the dorsum. The ventral trace of the adoral suture can not be made out on the specimen available for study, and Foerste shows only two sutures crossing the venter of the holotype; nevertheless,

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[15] Very little information is available in regard to the shell of any of the known representatives of this genus, but it should be mentioned that that of *Billingsites costulatus* (Whiteaves) bears both transverse bands and small transverse ridges, but the internal mold of its conch is smooth; the thickness of the shell in that species varies from ¼-½ mm. along the dorsum to nearly 1 mm. along the venter.

it seems probable that the adoral suture is essentially parallel to the preceding one along the venter and then coalesces with it along the ventro-lateral part of the conch. These two separate just orad of the strong reversal in their curvature on the dorso-lateral part of the conch, and as they gradually diverge orad, they are 3-5 mm. apart along the dorsum.

A median longitudinal section shows that the ventral two-thirds of the first (oldest) of these three adoral septa is almost straight (very slightly convex apicad), but the dorsal third is bent abruptly orad so as to form a broad shallow camera along slightly more than half of the dorsal part of the living chamber. The next septum is almost parallel to the first and throughout much of its length is almost in contact with it, but the two diverge slightly in the adapical end of the specimen and rather strongly in the adoral half of it. The adoral septum is almost parallel with the preceding one, but it coalesces with that septum a short distance (some 5 mm.) dorsad of the septal necks and then separates from it some 10 mm. in advance of there; the two diverge orad very gradually and are 3-5 mm. apart along the dorsum.

The nature of the siphuncle of the earlier stages of the phragmacone is not known, but that of the adoral ovoid portion of the conch is ventral in position and is moderately large; its segments are expanded so greatly within the camerae that they appear nummuloidal. The septal necks or funnels are very short and very strongly recurved; the connecting rings are parallel and almost in contact with the septa throughout most of their length. The siphuncle measures amout 4 mm. in diameter at its passage through the septum of truncation and expands to a diameter of about 9 mm. within the adjacent camera; it expands orad only very gradually, but its opening into the living chamber is much larger than that in the preceding septum and measures about 7 mm. in diameter.

Recently a considerable number of species has been referred to this genus, but it seems to the writer that they are not all congeneric with the above described genotype. Foerste has separated one group of them and proposed the generic name *Probillingsites* for it, and another group is distinguished below under the name *Schuchertoceras*; the latter is typified by *Billingsites anticostiensis* (Billings) and is characterized by the possession of a so-called "basal" septum between the septum of truncation and the strongly sigmoidal septa.

As near as can be told from the material available for study by the writer and the existing descriptions and figures, the following species possess the same general characters as *Billingsites canadensis,* the genotype of *Billingsites,* and should therefore be referred to that genus: *B. acutus* Foerste of the English Head (Richmond) of Anticosti Island, *B. elongatus* Foerste probably of the Ellis Bay (Gamachian) of Anticosti Island, *B. borealis* (Parks) of the Shamattawa (Richmond) of northeastern Manitoba southwest of Hudson Bay, *B. costulatus* (Whiteaves) of the Dog Head member of the Red River (Richmond) of southern Manitoba, *B. multicameratus* Miller and B. *bellicinctus* Miller of the Lander sandstone member of the Bighorn (Richmond) of west-central Wyoming, and *B. deformis* (Eichwald) of the Lyckholm (uppermost Ordovician or lowermost Silurian) of Dagö Island, Estonia.

Also, Foerste has mentioned in his recent publications that unnamed representatives of "*Billingsites*" occur in the Stony Mountain (upper Richmond) of southern Manitoba, the Ogonotz division of the Stonington (Richmond) of the peninsula east of Escanaba in northern Michigan, the base of the Whitewater (Richmond) of southwestern Ohio and adjacent parts of Indiana, the Maquoketa (Richmond) of northeastern Iowa, the Kallholn or Upper Leptaena limestone (uppermost Ordovician or lowermost Silurian) at Dalbyn in the Dalarne area of central Sweden, and the Gastropod limestone (uppermost Ordovician or lowermost Silurian) of the Ringerike area southwest of Oslo, Norway; three species are known to be represented at the last locality listed. Part of these forms doubtlessly represent *Billingsites* s.s. and part the genus described below as *Schuchertoceras,* but the published information in regard to them is not sufficient to allot them.

In summary then it can be stated that *Billingsites* is widely distributed in North America and is represented in Estonia and doubtlessly in southern Scandinavia. It is confined to the Upper Ordovician (Richmond and Gamachian) in North America, but in northwestern Europe it probably occurs in the Lyckholm of Estonia and the Gastropod limestone of Norway, which are either uppermost Ordovician or basal Silurian; their age is at present a moot question. Apparently this genus developed out of *Probillingsites* after the close of the Middle Ordovician in an arctic or subarctic sea, probably a branch of the northern Atlantic, and spread from there southward into North America and northwestern Europe during the latter part of the Upper Ordovician.

Billingsites differs from its progenitor, *Probillingsites,* in that its adoral sutures are much more complex; those of *P. primus* (Fritz), the most highly developed representative of *Probillingsites* known, are only slightly sigmoidal and there is no strong reversal in their curvature on the dorso-lateral walls of the conch as there is in *Billingsites.* The conch of *Shamattawaceras* is shaped differently, and its sutures are comparable in their complexity to those of *Probillingsites.* Comparisons with later derivatives of this stock are given below in the discussions of the genera concerned.

Genus SCHUCHERTOCERAS Miller, n. gen.

Plate III, Figs. 4-9

As mentioned above in the discussion of *Billingsites,* part of the species that have been referred to that genus are characterized by the possession of a so-called "basal" septum between the septum of truncation and the strongly sigmoidal adoral septa. These seem to constitute a natural group, and the generic name *Schuchertoceras*[16] is here proposed for it and *Billingsites* [*Ascoceras*] *anticostiensis* (Billings) of the English Head and Vauréal (Richmond) and Ellis Bay (Gamachian) of Anticosti Island is designated as the genotype. It is true that the biological significance of this "basal" septum is not as yet fully understood, but since, as is shown below, its presence or absence can be used to distinguish two closely related groups that became distinct after the Middle Ordovician and underwent parallel evolution during the Late Ordovician and Middle Silurian, its taxonomic value is obvious. It should not be imagined that the basal septum can be explained merely by assuming truncation along a more posterior septum; its development was much more complicated than that, and specimens from which the "basal" camera has been broken away do not resemble representatives of *Billingsites*—their incompleteness is obvious. Furthermore, as far as is now known, the choice of the septum along which truncation occurred in the mixochoanitic cephalopods was not left to chance but was predetermined, and (with

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[16] Named in honor of Professor Charles Schuchert, who fomented and fostered much of the recent geological work in southeastern Canada, whence came most of the known representatives of this genus.

the possible exception of *Choanoceras*) the septum of truncation invariably marked the junction of the adolescent part of the conch, in which the siphuncle was orthochoanitic in structure, with the mature part, in which it was cyrtochoanitic.

The holotype of *Schuchertoceras anticostiense* was originally referred by Billings (1862, p. 164) to "*Ascoceras Newberryi,*" but was later (1866, p. 60) recognized by him as representing a distinct species and given a specific name. Unfortunately it has since been lost. Foerste (1928, pp. 259-260) recently designated a neoholotype (Canada Geol. Survey, 2334a2), and although it does not appear to the writer to be very similar to the original type as sketched by Billings, it is here accepted as the type of the species and is designated as the type of the new genus.

Only the adoral obese expansion of the conch is known, and it is comparable in shape to that of *Billingsites* s.s. but is somewhat shorter and less narrowly rounded apicad and is therefore less ovoid and more nearly globular in shape. As it is slightly depressed dorso-ventrally, it is broadly elliptical in cross section. The adoral neck-like extension of the living chamber is slightly more prominent than that of typical *Billingsites*, but the apertures of both are broadly elliptical in outline; their lateral diameters are distinctly longer than their dorso-ventral.

The scar or cicatrix of attachment of the earlier stages of the phragmacone to the known portion of the conch (i.e., the impression of the septum of truncation) is not preserved on most of the numerous specimens of the type species available for study, but on one of them (Yale Peabody Museum, 3807b), which is strikingly similar to the neoholotype, it is very distinct. It shows that the septum of truncation of that specimen was moderately convex apicad and was strongly inclined to the long axis of the conch; it sloped orad from the venter. The ventral half of the suture of that specimen is normal, i.e., broadly rounded, but near the center of the lateral sides of the conch the suture curves rather strongly dorsad and continues, almost transverse to the long axis of the conch, across the dorsum approximately midway between the apex of the specimen and the basal suture; the scar of the septum of truncation is therefore more strongly convex ventrally than dorsally and is subelliptical in outline. The next septum orad, the so-called basal septum is essentially circular in outline. Its suture is almost parallel to that of the preceding septum along the venter but is slightly sigmoidal laterally, and the two sutures converge slightly on the ventro-lateral part of the conch and diverge markedly on the dorso-lateral; in the specimen under consideration they are about 3½ mm. apart along the venter, 1½ mm. near the center of the lateral sides, and 11½ mm. along the dorsum. The suture of the next septum is close to that of the basal septum and almost parallel with it along the ventral half of the conch, but near the center of the lateral sides of the conch, it bends abruptly orad and ventrad and continues in that direction to the center of the ventro-lateral sides of the conch, where it gradually ceases to swing ventrad and then curves rather abruptly dorsad and continues across the dorsum as an essentially straight line approximately transverse to the long axis of the conch; it crosses the dorsum about 15 mm. orad of the point where the basal suture crosses it. The adoral suture is very close to the preceding suture along the venter and apparently coalesces with it along the ventro-lateral sides of the conch. The two separate again near the mid-point of the ventro-lateral part of the conch and continue across the dorsum as two essentially parallel lines relatively close together.

A longitudinal section through the siphuncle shows that the basal septum is only very slightly convex and is inclined to the long axis of the conch at some forty-five degrees. The next septum is only about 1 mm. from the preceding one along the venter, but it diverges slightly from it in the vicinity of the septal necks; immediately dorsad of the necks the two septa converge slightly until they are almost in contact and then diverge markedly as the septum under consideration gradually curves orad and, after swinging slightly ventrad, curves dorsad again to meet the dorsum far orad of the point where the preceding septum meets it. The adoral septum is not well preserved in the ventral part of the sections available for study, but it appears to coalesce with the preceding septum slightly ventrad of the siphuncle, and it separates from it only in the extreme dorsal part of the conch, some 5-10 mm. below the dorsum. Foerste has recently (1928) figured a specimen that shows three septa orad of the basal septum and referred it to this species, but the shape of its conch as well as its sutures is so different from that of the neoholotype that the writer doubts that they are conspecific.

The earlier stages of the phragmacone and the siphuncle of this genus are not known, but in the known portion of the conch of the genotype the siphuncle is ventral in position and is relatively small at its passage through a septum but is expanded transversely within the camerae; the septal necks are short and strongly recurved. The connecting ring between the septum of truncation and the basal septum is moderately expanded transversely between the septa, but it is constricted centrally which suggests that during the development of the individual a septum that was later resorbed was formed midway between these two septa. The next and most adoral segment of the siphuncle is much more strongly expanded within the camera and is not constricted centrally.

As near as can be told from the material available for study and the published descriptions and figures, which refer almost exclusively to external features, the following species possess the same general characters as the above described genotype and should therefore be referred to *Schuchertoceras*: *Billingsites* [*Ascoceras*] *newberryi* (Billings)[17] of the English Head (Richmond) of Anticosti Island; *Billingsites logani* Cooper of the Upper Ordovician of the eastern part of Gaspé Peninsula, Quebec; *Billingsites troedssoni* Foerste of the Kallholn or Upper Leptaena limestone (uppermost Ordovician or lowermost Silurian) of the Dalarne area northwest of Stockholm, Sweden; and *Ascoceras norwegicum* Barrande or southeastern Norway, presumably from the Gastropod limestone (uppermost Ordovician or lowermost Silurian). Also, as explained above, part of the undescribed species of "*Billingsites*" that are known to occur in the Upper Ordovician of southern Manitoba, northern Michigan, southwestern Ohio and adjacent parts of Indiana, and northeastern Iowa, and in the uppermost Ordovician or lowermost Silurian (Kallaholn or Upper Leptaena, and Gastropod limestones) of the Dalarne area of central Sweden and the Ringerike area southwest of Oslo, Norway, doubtlessly represent this genus and part *Billingsites* s.s., but the published information in regard to them is not sufficient to allot them.

In summary then it can be stated that this genus is confined to the Upper Ordovician (Richmond and Gamachian) in North America but is known to occur in southeastern Norway and in the

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[17] Billings (1862, p. 165) lists this species as occurring also on the south side of the St. Lawrence opposite Three Rivers (Trois Rivières), Quebec, and at Point Rich, Ontario, in Lake Huron, but it is doubtful if the forms occurring at these two localities are conspecific with the types, which came from Anticosti Island, as the three localities are widely separated. The single poorly preserved specimen from the Niagaran of Delphi, Indiana, that Newell referred to this species is undoubtedly not congeneric with it.

Kallholn or Upper Leptaena limestone of Sweden where it is either uppermost Ordovician or lowermost Silurian in age. At present it is definitely known to occur only in southeastern Canada and southern Scandinavia, but in all probabilities it will eventually prove to be as widespread as *Billingsites* s.s., with which it is found in association. It seems probable that both of these genera developed out of *Probillingsites* after the close of the Middle Ordovician in an arctic or subarctic arm of the Atlantic and spread from there southward into northeastern North America and northwestern Europe during the latter part of the Upper Ordovician.

Genus LINDSTROEMOCERAS Miller, n. gen.

Plate V, Figs. 1-6

In his excellent study of the Ascoceratidae and the Lituitidae of the Silurian of Gotland, Lindström described two species of ascoceratoids from the zone of *Stricklandinia lirata* (lower Middle Silurian), a lower horizon than that which has yielded most of the Silurian ascoceratoids. He (p. 17) recognized that these forms presented certain striking differences from typical *Ascoceras* of the upper Middle Silurian of Bohemia, but he was too cautious to propose a generic name for them. Since the time of the publication of his memoir, our knowledge of the Ordovician mixochoanitic cephalopods has been increased many fold, and it now seems that, as is to be expected from the horizon they occupy, these lower Middle Silurian forms are clearly intermediate between part of the Upper Ordovician forms (*Schuchertoceras*) and part of the upper Middle Silurian forms (*Parascoceras*, described below); nevertheless, they appear to be generically distinct from both, and the generic name *Lindstroemoceras* is here proposed for them and L. [*Ascoceras*] *dolium* (Lindström) from Lindström's formation "b" near Visby, Gotland, is designed as the genotype.

Only the adoral obese part of the conch of this species is known, and our knowledge of it is based on two specimens. The conch is small, breviconic, and cyrtoceraconic, and the known portion is subovate in shape as it is short, obese, abruptly contracted orad, and more gradually so apicad; it is distinctly compressed laterally and is broadly elliptical in outline, but its ventral side is somewhat more convex than its dorsal. The adoral part of the conch is projected into a short neck-like extension, but its length and the nature of the aperture are not known as neither of the types is complete adorally.

The surface of the internal mold is crossed by numerous small transverse ridges which curve slightly apicad as they cross the venter; they are somewhat less than 1 mm. apart. Both of the types retain traces of five septa; the adapical two, the septum of truncation and the basal septum are normal, saucer-shaped nautiloid septa, moderately convex apicad, and slightly inclined to the long axis of the conch; they slope orad from the venter. The next septum is close and almost parallel to the preceding ones in the ventral half of the conch, but near the mid-height of the conch it bends abruptly orad and continues in that direction to the center of the specimens where it bends abruptly dorsad and meets the dorsum near its mid-length. The next septum is very close and approximately parallel to the preceding one in the adapical half of the specimens, but near the center of them, where the preceding septum curves dorsad, this septum curves ventrad and orad and then gradually ceases to swing ventrad and curves dorsad; it meets the dorsum near the base of the adoral neck-like extension of the living chamber, far orad of the preceding septum. The adoral septum is not complete; it coalesces with the preceding septum just dorsad of the siphuncle and apparently becomes distinct from it again only in the extreme adoral part of the conch.

The nature of the siphuncle of the earlier stages of the phragmacone is not known, but in the adoral ovoid expansion of the conch it is ventral in position and is moderately small but it gradually increases in diameter orad. The septal necks apparently are short and strongly recurved. The segment of the siphuncle between the septum of truncation and the basal septum is expanded within the camera, and the connecting ring is subfusiform in shape; those of the adoral segments are not preserved in either of the types, but they probably were subnummuloidal in shape.

The general shape of the conch and the sutures of *Ascoceras cochleatum* Lindström of the soft gray shale (Lindström's formation "b" = lower Middle Silurian) near Visby, Gotland, are strikingly similar to that of the above-described genotype, and therefore that species is regarded by the writer as belonging to the genus under consideration although its conch is strongly annulated. The single fragmentary specimen found in the "red limestone [upper Middle Silurian] at Holms haller in Wamlingbo," Gotland,

and regarded by Lindström as a doubtful variety of this species only because of a similarity in surface sculpture, probably does not belong to this genus but to *Aphragmites*, and no other species is known to the writer that should be referred to this genus.

The fact that the adoral expansion of the conch of this genus is very short and obese and is subovoid in shape is indicative of a close relationship to the Upper Ordovician and Lower Silurian mixochoanites, but the lateral compression, adapical attenuation, and moderately long and distinct adoral extension of the living chamber indicate a relationship to the upper Middle Silurian ascoceratoids; the genus seems to be distinctly intermediate between *Schuchertoceras* of the Upper Ordovician and probably the Lower Silurian and *Parascoceras* of the upper Middle Silurian. The presence of a basal septum serves to distinguish it from *Billingsites* of the Upper Ordovician (and possibly the Lower Silurian) and *Ascoceras* s.s. and *Aphragmites* of the upper Middle Silurian.

Genus PARASCOCERAS Miller, n. gen.

Plate VII, Figs. 3-12

Of the numerous ascoceratoids known from the upper Middle Silurian, only one[18] species, *Ascoceras fistula* Lindström of the uppermost formation (Lindström's "stratum h") of Gotland, possesses a so-called basal septum, i.e., a septum between the septum of truncation and the first sigmoidal septum. Lindström called attention to this fact and he realized that the possession of this septum indicated a close relationship between this species and the forms from the lower Middle Silurian termed *Lindstroemoceras* above, but he apparently attached little importance to it. The significance of this basal septum is treated of elswhere in this report but perhaps it should be mentioned here that the presence or absence of it enables us to distinguish two closely related stocks

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[18] The specimen, showing two septa apicad of the first sigmoidal one, that Barrande (1877, pp. 98 99, pl. 491, figs. 3-7) described and figured and referred to *Ascoceras murchisoni* was regarded by Lindström (pp. 18-19) as indicating a close relationship between that species and *Ascoceras fistula*; but in the writer's opinion that specimen is either abnormal, in that truncation accidently took place slightly apicad of the adoral end of the orthochoanitic part of the conch instead of at the junction with the cyrtochoanitic part, or it is an immature individual in which the adapical portion of the conch had not been broken off as yet and only the two adoral camerae of it were preserved. The septum regarded by Lindström as homologous with the so-called basal septum of *A. fistula* is not close to the first sigmoidal septum but is relatively far from it, and the segment of the siphuncle between the two was undoubtedly cylindrical and not nummuloidal.

that differentiated in the Ordovician and evolved along parallel lines until near the close of the Middle Silurian, when both became extinct. It should also be repeated here for the sake of emphasis that as far as is now known, the septum of truncation in the mixochoanitic cephalopods (with the possible exception of *Choanoceras*) marks the junction of the orthochoanitic part of the conch with the cyrtochoanitic, and therefore the presence of a basal septum can not be explained merely by assuming truncation along a more posterior septum; its development was far more complicated than that.

As is obvious from what has been stated above, this species represents a genus that is quite distinct from typical *Ascoceras*, though it resembles that form in many respects, and the name *Parascoceras* is here proposed for it; *P.* [*Ascoceras*] *fistula* (Lindström), the only known species, is the genotype. That form is known to occur only in one horizon in Gotland, but it is comparatively abundant there and Lindström figured a slab only two or three inches square that contains twenty-one more or less perfect representatives of it.

As is probably the case with most of the other mixochoanitic cephalopods, the conch of this species consists of two distinct parts. The adapical tubular part, termed the "Nautiloid stage of growth" by Lindström because its septa are normal saucer-shaped disks approximately transverse to the long axis of the conch, is here called the orthochoanitic part. The adoral portion of the conch in which all of the septa but the so-called basal septum are strongly sigmoidal, is termed the "Ascoceras stage" by Lindström, but it is here called the cyrtochoanitic part of the conch; it includes the living chamber as well as the cyrtochoanitic part of the phragmacone of mature specimens. The septum of truncation apparently formed the junction of these two parts, and the two have never been found connected; nevertheless, the similarity of their size and surface sculpture, the position of their siphuncles, and the fact that the two are found only in very close association indicate that they represent the same species, and that the adapical portion of the conch was truncated during the life of the individual.

The orthochoanitic part of the conch is long, narrow, tubular, and almost straight, and it is only very gradually expanded orad; it is circular or nearly so in cross section. The protoconch is not known, and the adapical end of the conch is bluntly rounded. The surface of the conch is crossed by numerous, low, rounded, inconspicuous transverse ridges, which are considerably less than 1 mm. apart and which curve slightly apicad as they cross the venter; the surface of these ridges and the concave spaces between them is finely transversely striate. The septa are moderately convex apicad and are approximately transverse to the long axis of the conch but slope slightly orad from the venter; the sutures are simple and straight and approximately circular. They are moderately close together, but the distance between them increases progressively orad. The siphuncle is ventral in position and is small. The septal necks are very short, but they are not recurved and the connecting rings are not expanded transversely within the camerae but are cylindrical in shape.

The adoral or cyrtochoanitic part of the conch at maturity consists of the living chamber and four camerae. It is slightly curved longitudinally and is long, narrow, and subcylindrical in shape, but it is somewhat compressed laterally and is therefore broadly elliptical in cross section. Its maximum transverse dimensions are attained somewhat apicad of its mid-length, and it is contracted slightly both orad and apicad of there. The adoral end of the living chamber is projected orad into a long cylindrical neck-like extension, which is circular in cross section and constitutes about two-sevenths of the total length of the living chamber. The surface of the conch is marked by numerous small transverse ribs about ⅓ mm. apart; these curve slightly apicad as they cross the venter, and they are finely striate. The septum of truncation and the basal septum are very similar to the septa of the orthochoanitic part of the conch and are normal, saucer-shaped, nautiloid septa that are approximately transverse to the long axis of the conch but slope slightly orad from the venter. The next septum is approximately parallel to the basal septum in the ventral half of the conch, but in the dorsal half it curves strongly orad and then slightly ventrad, and, near the mid-length of the specimen, curves strongly dorsad to meet the dorsum. With the exception of a single specimen figured by Lindström, in which the first two sigmoidal septa are entire, the two adoral septa are not complete centrally as they unite and then coalesce with the preceding septum just dorsad of the siphuncle and separate from it only in the adoral half of the conch; they extend the phragmacone along the dorsum to the base of the neck-like adoral extension of the living chamber mentioned above. This coalescing of the sigmoidal septa is visible only in sectioned specimens, for the edges of all these septa are distinct and their sutures do not coalesce. It is interesting to note in this connection that in senile representatives of this genus, as in those of *Ascoceras* s.s. and *Pseudascoceras*, an additional septum, here termed an *adventitious septum*, is added in the posterior end of the living chamber close to the adoral sigmoidal septum; no trace of it is visible along the dorsum as it coalesces with the preceding septum in the dorsal part of the conch. The siphuncle of this cyrtochoanitic part of the conch is ventral in position and is moderately small, but its segments are expanded transversely within the camerae. The septal funnels apparently are short and strongly recurved, and the connecting rings are subspherical in the posterior part of the specimen but become much shorter in the adoral part, where they are asymmetrically subnummuloidal. The septal necks and connecting rings of the adventitious septum present in senile individuals are similar to those of the preceding septa.

As mentioned above, no species is known to the writer that is congeneric with this genotype, and its closest relatives seem to be the three forms discussed below and referred to a new genus, *Pseudascoceras*, in which the basal septum apparently was resorbed before the individuals attained maturity. It is believed by the writer that both this form and *Pseudascoceras* evolved from *Lindstroemoceras* of the lower Middle Silurian, which is a shorter and more obese form with a much shorter and less distinct neck or adoral extension of the living chamber. The presence of a basal septum serves to distinguish the genus under consideration from other similar genera.

Genus Pseudascoceras Miller, n. gen.

Plate V, Figs. 7-21

As mentioned above in the discussion of *Parascoceras*, three of the numerous species of ascoceratoids described by Lindström from the upper Middle Silurian of Gotland apparently possessed a basal septum during part of their development but resorbed it before attaining maturity. These forms then are closely related to *Parascoceras* and *Lindstroemoceras*, which retained the basal septum throughout life, but externally they appear to resemble much more closely *Ascoceras* s.s., which never possessed a basal septum. They obviously are generically distinct from all three of the genera mentioned, and the generic name *Pseudascoceras* is here proposed for them and *P.* [*Ascoceras*] *decipiens* (Lindström) of the uppermost formation of Gotland (Lindström's "stratum h") is designated as the genotype.

That species is known from numerous specimens from various localities on the island of Gotland. Its conch consists of two distinct parts; the adapical one is orthochoanitic, the adoral cyrtochoanitic. The former was generally broken off during the life of the individual, but both parts are known and have been found connected in immature representatives.

The orthochoanitic part of the conch is moderately long, narrow, and very gradually expanded orad; it is distinctly curved exogastrically, but the amount of curvature decreases adorally. The protoconch is not known, and the bluntly rounded apex of the conch does not show any distinct cicatrix. The surface of this orthochoanitic part of the conch is finely transversely striate and in addition bears small, low, rounded, indistinct longitudinal ridges. The septa are saucer-shaped and moderately convex apicad. They are rather close together, but the distance between them varies somewhat and in general increases progressively orad. They are transverse to the long axis of the conch, and the sutures are therefore simple circles. The siphuncle is small, circular in cross section, and ventral in position. The septal necks are short but are not recurved, and the connecting rings are cylindrical in shape; therefore the segments of the siphuncle are not expanded appreciably within the camerae.

The adoral or cyrtochoanitic part of the conch of mature specimens consists of the living chamber and four camerae. It is slightly curved exogastrically, and is long, narrow, and subcylindrical in shape, but it is slightly compressed laterally and is therefore broadly elliptical in cross section. It is nearly straight along the dorsum but is convex along the venter. Its maximum transverse dimensions are attained near the mid-length of the living chamber proper, and it is somewhat contracted apicad and slightly so orad of that point. The adoral end of the living chamber is projected into a long narrow tubular neck that is circular in cross section and is distinctly inclined to the long axis of the conch; its maximum length and the nature of the aperture are not known, but it is at least two-fifths as long as the living chamber proper. The entire cyrtochoanitic part of the conch is finely transversely striate and is marked also by small, low, rounded longitudinal ridges. The ornamentation varies slightly in the different parts of the conch; it is finer on the ventral and apical portions of the specimens and is coarser on the neck. The septum of truncation is asymmetrically subconical and is inclined to the long axis of the conch; it slopes orad from the venter. The next septum is approximately parallel to it in the ventral three-fourths of the conch, but its dorsal part curves abruptly orad and then somewhat ventrad and continues in that direction to the center of the living chamber proper, whence it curves abruptly dorsad to meet the dorsum. The next four septa are not complete centrally as they unite and then coalesce with the first sigmoidal septum just dorsad of the siphuncle and become distinct from it again only in the adoral half of the conch; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. This coalescing of the septa is visible only in sectioned specimens, for the edges of all the sigmoidal septa and therefore the sutures are distinct. Lindström observed a thin deposit that he believed to be organic in origin on the inside of the living chamber extending a short distance each side of the junction of the adoral septum with the dorsum, but the significance of this is not understood. The siphuncle of this part of the conch is small at its passage through a septum, but the segments are greatly expanded transversely within the camerae. A small oblique narrow tube connects the siphuncles of the two parts of the conch. The septal necks are short and strongly recurved. The connecting ring between the septum of truncation and the first sigmoidal septum is almost square in longitudinal section, but near its mid-length it bears a constriction, comparable to that observed in *Schuchertoceras*, but angular on the ventral side and rounded on the dorsal. This segment of the siphuncle is more than twice as long as the succeeding ones, and the constriction near its mid-length is interpreted by the writer as a vestige of a septum—comparable to the basal septum of *Parascoceras* and *Lindstroemoceras*—that was present during part of the development of the individual but was resorbed before maturity. This constriction is therefore regarded as one of the most significant of the generic characters, and it indicates that this form is much more closely related to the two genera mentioned above than to *Ascoceras*, to which it is strikingly similar externally. The adoral four segments of the siphuncle are much shorter and are subnummuloidal in shape; they become progressively shorter orad.

It is exceedingly important to note that a senile individual of this species has been described by Lindström in which as many as four adventitious septa are present "in the adapical part of the living chamber." These are all normal, saucer-shaped nautiloid septa, strongly convex apicad, and slightly inclined to the long axis of the conch; they slope orad from the venter. The septal necks of the first two of these septa are strongly recurved, and the connecting ring of the first is asymmetrically subnummuloidal in shape, whereas that of the next is asymmetrically fusiform. The septal necks of the two adoral septa, however, are not recurved, and their connecting rings are only slightly expanded transversely within the camerae. The important thing to note in this connection is that this particular individual has reverted to an orthochoanitic form after passing through a cyrtochoanitic stage. The significance of this is more or less of an open question, but it seems to the writer that this demonstrates that the distinction between cyrtochoanitic and orthochoanitic forms is not as great as most paleontologists are inclined to believe.

It should also be noted that other representatives of this species have been described by Lindström that indicate that the adoral part of the conch was completed by the individual before the sigmoidal septa were developed and truncation occurred. One specimen represents an immature individual which had secreted only the first of the sigmoidal septa and had not broken off the adapical portion of the conch; the adoral connecting ring of this specimen bears the characteristic constriction near its mid-length and demonstrates that, as would be expected, the assumed basal septum was resorbed before the sigmoidal septa were formed.

As is indicated by the name and has been explained above, representatives of this genus can be differentiated from typical *Ascoceras* only by means of internal structures, i.e., vestiges of a basal septum; therefore only those species in which the details of the siphuncle are known can be definitely allotted. As far as the writer has been able to ascertain, only *Ascoceras sipho* Lindström and *Ascoceras gradatum* Lindström, both of the Upper Middle Silurian (Lindström's "stratum h") of Gotland have been shown to possess similar vestiges of a basal septum and therefore to belong to this genus. In the future it may be possible to show that some of the numerous species at present assigned to *Ascoceras,* actually represent this genus, but until representatives of those forms have been sectioned and studied, it will be best to leave them in the genus to which they have been referred.

Genus ASCOCERAS Barrande 1847

[= *Cryptoceras* Barrande (1846) 1847, but not *Cryptoceras* D'Orbigny 1850]

Plate VI, Figs. 1-6; Plate VII, Figs. 1,2; Plate VIII, Figs. 10,11

A detailed summary of the development of our knowledge of this genus has been ably presented by Barrande and later by Lindström, and therefore it will suffice here to mention only the more significant points. In 1846 Barrande announced the discovery of this genus and proposed the name *Cryptoceras* for it; however as he then stated only that it is a "genre que nous avons créé pour classer des formes auparavant inconnues et très-bisarres," he failed to establish the name, for this statement can not be considered a generic diagnosis and it is not accompanied by an illustration. In the following year Barrande abandoned the name *Cryptoceras* as he believed it was too similar to *Cryptocerus* Latreille, a hymenopterous insect, and he proposed to call his genus *Ascoceras;* this time he gave a concise diagnosis of the genus and established its name as *Ascoceras.* It was not necessary for him to abandon *Cryptoceras,* but in as much as he did so before it was established, i.e., while it was a *nomen nudum,* that term can not be revived on the grounds of priority, as has recently been suggested by Schindewolf (1929, p. 171). Furthermore, since in the same publication in which *Ascoceras* is established, it is stated that Barrande's term *Cryptoceras* referred to the same genus, that name also is established, and it must be regarded as a direct synonym of *Ascoceras;* it was "stillborn and can not be brought to life." According to Barrande (1867, p. 335) the above-mentioned original diagnosis of *Ascoceras* was "imprimée d'abord dans *Oesterr. Blätt. für Litt. u. Kunst* en 1847 et ensuite dans *Haidinger's Berichte III, p. 268,*" 1848. The writer has not been able to locate a copy of the first of these two references, but Barrande's statement is confirmed by the editor of the second.

In manuscript prepared in 1847 but not published until 1850, D'Orbigny[19] unaware of Barrande's earlier use of the term *Cryptoceras,* employed it for an entirely different group of nautiloids, according to him known to be represented by one Devonian and one Carboniferous species; and in the second edition of Woodward's *A manual of the Mollusca . . .*, London, 1866 (p. 189). *Ascoceras* Barrande is inadvertently listed as a synonym of *Cryptoceras* D'Orbigny. In his *Prodrome de Paléontologie . . .* (vol. 1, p. 58 and p. 114, 1850), D'Orbigny listed as the two species on which he had based his genus *Nautilus subtuberculatus* G. and F. Sandberger of the Devonian of Germany and *Nautilus dorsalis* Phillips of the Carboniferous of England. In 1883 Hyatt (p. 283) designated the former as the type of the genus, which, however, he regarded as a synonym of *Temnocheilus* M'Coy 1844; *Nautilus* (*Temnocheilus*) *coronatus* M'Coy of the Carboniferous of Ireland is the type of *Temnocheilus.* The types of these two genera are not very similar, and the modern refinement in limiting nautiloid genera makes it expedient to resurrect D'Orbigny's genus, but in view of the fact that the name employed by D'Orbigny was preoccupied, it is necessary to coin a new generic name for the genus, and it is here proposed to call it *Nassauoceras;* the type species, *N.* [*Nautilus*] *subtuberculatus* G. and F. Sandberger[20], came from the Devonian of Nassau, a former duchy of Germany.

In 1855 Barrande for the first time named and described a species of *Ascoceras, A. bohemicum* of the upper Middle Silurian of Bohemia (since found also in the upper Middle Silurian of Gotland), and it is the type of his genus. Only the adoral or cyrtochoanitic part of the conch of this species is known; it has been described in detail by Barrande, Lindström, and Foord, and therefore the following concise description will suffice here.

The known portion of the conch of this species, the adoral cyrtochoanitic part, in typical, mature specimens consists of the living chamber and the adoral four (sometimes five) camerae of the phragmacone. It is subcylindrical in shape but is convex exteriorly and, as it is compressed laterally, is oval in cross section; it is more narrowly rounded ventrally than dorsally. The adoral fifth

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[19] D'Orbigny, Alcide, Cours élémentaire de Paléontologie et de Géologie stratigraphiques, vol. 1, p. 286, Paris, 1849 (not published until 1850 according to Barrande [1867, p. 335]).

[20] Originally described by Sandberger, Guido, and Sandberger, Fridolin, Die Versteinerungen des rheinischen Schichtensystems in Nassau, pp. 133-134, pl. 12, figs. 3a-3e, Wiesbaden, 1850-1856.

of the living chamber is projected aperturally into a neck-like extension that is circular in cross section and is inclined to the long axis of the conch; the aperture is circular and is directly transverse to the long axis of the neck and therefore inclined to that of the conch. The test is moderately thick and is finely transversely striate. The septum of truncation is a normal saucer-shaped nautiloid septum that is only slightly convex apicad and is distinctly asymmetrical; it slopes orad from the venter and is therefore inclined to the long axis of the conch. The next septum is not far orad of the septum of truncation and is approximately parallel to it in the ventral four-fifths of the conch, but slightly below the dorsum it curves orad and ventrad and continues in that direction to near the mid-length of the living chamber proper, where it curves abruptly dorsad to meet the dorsum. The next four septa are not complete centrally as they unite and then coalesce with the first sigmoidal septum just dorsad of the siphuncle and become distinct from it again only in the adoral half of the specimens; they extend the phragmacone along the dorsum almost to the base of the adoral neck of the living chamber. The maximum dorso-ventral thickness of the adoral portion of the phragmacone is attained somewhat orad of the mid-length of the living chamber proper along the third camera, and the adoral segment of the phragmacone is much smaller than the preceding ones. The details of the coalescing of the septa vary in different individuals and apparently in some cases (see Lindström, pl. 3, and Barrande, pl. 494) it can be observed only in sectioned specimens as the edges of the septa and therefore the sutures are distinct. However, Barrande figured one specimen (pl. 93) in which the two adoral sutures coalesce laterally, and another (pl. 513) in which all of the sigmoidal septa coalesce successively along the lateral sides of the conch. The sutures of the sigmoidal septa curve slightly apicad on the dorso-lateral sides of the conch and form broad, shallow median lobes along the dorsum; these however become less prominent adorally. The siphuncle of this part of the conch is ventral in position and is moderately large, but it apparently decreases in diameter adorally. The septal necks are fairly short and are strongly recurved; the connecting rings are greatly expanded transversely within the camerae, and the segments of the siphuncle are asymmetrically subnummuloidal in shape.

As mentioned above, the earlier stages of the phragmacone of this species are not known, but they doubtlessly were very similar to those of *Ascoceras manubrium* Lindström and *Ascoceras lagena* Lindström, which have been found in connection with the adoral portion of the conch. The adapical or orthochoanitic part of the conch of both of those species is long, narrow, very gradually expanded orad, and gently curved exogastrically. Neither the protoconch nor the adapical end of the phragmacone is known. The sutures are simple circles and the septa are normal saucer-shaped nautiloid septa moderately convex apicad and approximately transverse to the long axis of the conch; they are fairly close together in the adapical part of the conch, but the distance between them increases progressively orad and equals or exceeds the diameter of this portion of the conch near its junction with the cyrtochoanitic portion. The siphuncle is small and is located close to the ventral wall of the conch. The septal necks are short but are not recurved, and the connecting rings are not expanded appreciably within the camerae but are cylindrical in shape.

The conch of the above described genotype, *Ascoceras bohemicum,* is somewhat larger than that of most of the forms that have been referred to this genus, but as near as the writer has been able to determine from the literature and the material available for study, the following species possess the same general characters and should therefore be referred to *Ascoceras* s.s.,: *A. bronni* Barrande[21], *A. murchisoni* Barrande, *A. singulare* Barrande, and *A. verneuili* Barrande, all of Barrande's division "e2" of stage E (= Eβ of Kettner and Kodym) of the upper Middle Silurian of Bohemia; *Ascoceras* cf. *A. murchisoni* (identified by Perner, 1922, p. 60) of E1γ, that is, the passage beds (= Dubius beds of Perner) between e1 and e2 of Bohemia; *A. pupa* Lindström, *A. reticulatum* Lindström, *A. ampulla* Lindström, *A. collare* Lindström, *A. lagaena* Lindström, *A. manubrium* Lindström, and *A. cucumis* Lindström, all of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland; *A. barrandii* Salter of the Upper Ludlow of England; *A. southwelli* Worthen of the Port Byron of Illinois; *A. croneisi* Foerste of the Racine of Wisconsin; *A. indianensis* Newell of the Huntington of northern Indiana; and *A. townsendi* Whiteaves of the Guelph of southeastern Ontario. Also, the affinities of the following forms, which are

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[21] The forms originally described by Barrande as *Ascoceras* (*Aphragmites*) *salteri* were later correctly included by him in *Ascoceras bronni.*

based upon poorly preserved material and are therefore incompletely known seem to be with this genus rather than any of the other genera discussed in this report: *A. vermiforme* Blake from the Lower Ludlow (and Upper Ludlow?) of England; the specimen from the Upper Ludlow of Whitecliffe, England, that Blake (p. 208) incorrectly identified as *A. bohemicum;* the specimen from the Huntingdon of Delphi, Indiana, that Newell (p. 484) incorrectly identified as "*Ascoceras Newberryi* Billings"; and the various forms from the upper Middle Silurian of Gotland figured by Lindström (pl. 4) as *Ascoceras* spp. Additional material may enable us to allot these forms definitely in the future, but for the present it seems best to leave them in the genus to which they have been referred. In summary it can be stated that *Ascoceras* s.s. is known to be represented in the upper Middle Silurian of Bohemia, Gotland, England, Ontario, Indiana, Illinois, and Wisconsin. *A. townsendi* Whiteaves (figured on plate VIII, figures 10, 11, of this report) is the last representative of the group known to occur in North America.

The genus *Ascoceras* can be readily distinguished from *Glossoceras* by its simple aperture; from *Aphragmites* by its non-annulated conch; from *Billingsites* by its laterally compressed, subcylindrical conch with circular aperture and longer, more distinct neck; and from *Schuchertoceras, Lindstroemoceras, Parascoceras,* and *Pseudascoceras* by the absence of a basal septum or vestiges of it.

Genus Aphragmites Barrande 1865

Plate VIII, Figs. 1-9

As is indicated by its name, this genus was created by Barrande as a result of a misconception, i.e., during much of his study of the ascoceratoids, he believed that one group of them was essentially without septa. As early as 1855 he mentioned this view and figured *Ascoceras buchi* Barrande of the upper Middle Silurian of Bohemia as typical of the group, which, however, he did not name until 1865, when in a volume of plates (explanation of pl. 94) he wrote as follows: "Nous établissons le sous-genre *Aphragmites* pour comprendre les deux espèces: *Buchi* et *Salteri,* dans lesquelles il ne paraît exister qu'une seule cloison permanente, terminant la grande chambre, sans cloisons intermédiares." In the text to accompany these plates, published two years later, he (pp. 366-372) raised *Aphragmites* to generic rank, discussed it at some length, and described the two species that he had referred to it. However, in 1877, when he completed his voluminous masterpiece on the cephalopods, he (p. 94) renounced this genus, stating "nous concevons, que l'animal résorbait toutes les cloisons adossées à la grande chambre, à chacune des époques périodiques, qui correspondent à sa croissance et à l'agrandissement de son habitation. . . . En adoptant cette conception . . . nous avons été amené à regarder les coquilles dénuées de toute cloison interne et par ce motif, nommées par nous *Aphragmites,* comme représentant l'état transitoire, qui correspond à la transformation en question. Nous sommes donc obligé de considérer le genre *Aphragmites* comme désormais sans raison d'être et nous devons déterminer quelles sont les espèces du genre *Ascoceras,* auxquelles les 2 formes nommées: *Aphragm. Buchi* et *Aphragm. Salteri,* doivent être rapportées. Nous allons exposer pour chacune de ces 2 formes les motifs qui nous induisent à les incorporer, la première dans l'espèce *Ascoc. Deshayesi* et la seconde dans l'espèce *Ascoc. Bronni.*"

In 1883, Hyatt (p. 279) resurrected this genus, stating that he preferred Barrande's earlier opinion in regard to it, and in 1900 (p. 516) he recapitulated this view. Zittel (1885, p. 371) likewise took cognizance of it and considered it a valid genus, though he was cautious enough to mention Barrande's ultimate conclusions in regard to it.

However, it remained for Lindström to demonstrate the true nature of this misunderstood "genus" and to show that it in reality represented a developmental stage of *Ascoceras,* i.e., as an individual of that genus approached maturity it apparently underwent a metamorphosis and suddenly increased the diameter of the conch that it was secreting; the walls of this expanded adoral portion of the conch were then completed aperturally while septa were being formed in the narrow adapical portion of the conch. At or shortly after this stage in the development, the adapical septate portion of the conch was cast off and septa were formed in the apical and dorsal parts of the remaining (the expanded) portion of the conch. Just before these later septa were secreted, the conch was in the "Aphragmites stage" of development.

In spite of the fact that "*Aphragmites*" as originally conceived represented only a developmental stage of *Ascoceras,* it now seems desirable to retain the generic name; for as has already been noted by Foerste (1924, pp. 216-217), the conch (and the internal mold) of *Ascoceras buchi*, which has always been regarded as the type of *Aphragmites* and is here selected as such, is prominently annulated transversely, whereas that of typical *Ascoceras* is smooth or finely striate.

Only the adoral, expanded, or cyrtochoanitic part of the conch of the genotype, *Aphragmites* [*Ascoceras*] *buchi* (Barrande)[22] of stage E of the upper Middle Silurian of Bohemia, is known, and as it has been described in detail by Barrande (1867, pp. 361-362 and 370-371; 1877, pp. 94-95), the following concise description will suffice here. The earlier stages of the phragmacone, the orthochoanitic part of the conch, in all probability, were comparable to those of *Ascoceras* s.s.

The known portion of the cyrtoceraconic conch of this rare species consists in mature specimens of the living chamber and the adoral four camerae of the phragmacone. It is moderately small and is subfusiform in shape, but it is compressed laterally and is therefore elliptical in cross section. It is almost straight (very slightly convex) along the dorsum but is strongly gibbous along the venter; its maximum transverse dimensions are attained near its mid-length and it is rather strongly contracted both apicad and orad of that point. Its adoral portion is projected aperturally into a neck-like extension that is about one-third as long as the living chamber proper, is distinctly inclined to the long axis of the conch, and is circular in cross section. The aperture is simple and, as it is transverse to the long axis of the neck, is circular in outline. The test is moderately thin, and both it and the internal mold are strongly annulated transversely. The narrowly rounded annulae are about the same size as the intermediate grooves and are directly transverse to the long axis of the conch. They are about ½ mm. high and 1½ mm. apart in the central portion of the specimens, but they become less prominent and more closely spaced both adapically and adorally; they are rather faint and only about ½ mm. apart on the adoral neck. The septum of truncation is a normal, saucer-shaped nautiloid septum that is slightly inclined to the long axis of the conch; it slopes orad from the venter. The dorsal part of the next septum is bent strongly orad and slightly ventrad so as to form a very prominent deep dorsal saddle before it meets the dorsum slight-

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[22] This species and *Ascoceras deshayesi* Barrande are identical, and the older name is retained.

ly apicad of the mid-length of the living chamber proper. The nature of the rest of the septa in the ventral half of the conch is not known, but they probably unite and then coalesce with the preceding septum slightly dorsad of the siphuncle. Anyhow, they are not complete centrally, and they separate from the preceding septum and then from each other in the adoral half of the specimens; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. The maximum dorso-ventral thickness of this adoral dorsal portion of the phragmacone is attained somewhat orad of the mid-length of the living chamber proper along the adapical end of the adoral camera or the adoral end of the preceding one. The sutures of the second and third of these sigmoidal septa curve slightly apicad on the dorso-lateral sides of the conch and form shallow median lobes along the dorsum. All of these sigmoidal sutures appear to coalesce laterally near the same point in the adapical third of the specimens; unfortunately their nature on the ventral side of the conch is not known. The siphuncle is ventral in position and is moderately small at its passage through a septum, but it appears to be expanded within the camerae; nothing further is known in regard to it. The siphuncle and the ventral traces of the sigmoidal septa of this genus are probably not greatly different from those of *Ascoceras* s.s.

As near as can be told from the literature, the following species possess the same general characters at this genotype and should therefore be grouped together with it under the generic name *Aphragmites*: *Ascoceras goldfussi* Barrande, *A. invertens* Barrande, *A. keyserlingi* Barrande, *A. amoenum* (Barrande)[23], and *A. konincki* Barrande, all of the same general horizon and locality as the genotype, i.e., Barrande's division "e2" of stage E (= Eβ of Kettner and Kodym) of the upper Middle Silurian of Bohemia.

It seems likely that this genus arose from *Ascoceras* or its immediate progenitor by the increased prominence of certain of the transverse striae, and it is perhaps significant that it is not known to occur outside of Bohemia, with the possible exception of the single fragmentary specimen from the upper Middle Silurian of Gotland mentioned above in the discussion of *Lindstroemoceras*. It should also be noted in this connection that at least one of the known representatives of *Billingsites* [*B. costulatus* (Whiteaves)]

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[23] This form was described by Barrande as a variety of *Ascoceras keyserlingi*, but it is here regarded as a distinct species.

bears rather prominent transverse ridges on the exterior of its conch, but the internal mold is smooth; also transverse annulations were developed in at least one other group of the Mixochoanites, *Lindstroemoceras* of the lower Middle Silurian of Gotland.

The conch of this genus is strikingly similar to that of *Ascoceras*, from which it differs chiefly in being annulated, and it can be differentiated from other similar genera by the criteria mentioned at the close of the discussion of that genus.

Genus GLOSSOCERAS Barrande 1865

Plate VIII, Figs. 12-25

This genus was established by Barrande in a volume of plates (explanation of plate 94) as a subgenus of *Ascoceras*, and defined as follows: "Nous établissons le sous-genre *Glossoceras*, pour comprendre les formes dont l'ouverture est contractée par une languette, comme celle des *Lituit. Ophioceras*, et reproduit à peu-près le type de l'ouverture des *Phragmoceras* et *Gomphoceras*." The text to accompany these plates did not appear until two years later, and in it Barrande (pp. 372-375) raised *Glossoceras* to generic rank, discussed it at some length, and described in detail one species and a variety of it (here regarded as two distinct species). Since then Barrande, Hyatt, Zittel, Foord, and other authors have discussed this genus at various times, but only Lindström has added appreciably to our knowledge of it. He found a representative of it in the upper Middle Silurian of Gotland and studied its internal structure in detail, which Barrande had failed to do.

The single species recognized by Barrande, *Glossoceras gracile* (Barrande) of division "e2" of stage E (= Eβ of Kettner and Kodym) of the upper Middle Silurian of Bohemia, is the type of the genus. Only the adoral or cyrtochoanitic part of its conch is known, but the earlier stages of its phragmacone, i.e., the orthochoanitic part of the conch, in all probability, were comparable to those of *Ascoceras* s.s. In as much as this genotype has been described in detail by Barrande the following concise description will suffice here.

The known portion of the conch of this species, the adoral or cyrtochoanitic part, consists in mature specimens of the living chamber and the adoral six camerae of the phragmacone. It is long and slender and is somewhat curved exogastrically; it is compressed laterally and, being more narrowly rounded ventrally than dorsally, is oval in cross section. The adoral fifth of the living chamber is projected aperturally into a long, narrow cylindrical neck that is circular in cross section; this neck is distinctly curved endogastrically, and therefore the specimens as a whole are sigmoidal in shape. The dorsal side of the aperture is projected as a moderately long and narrow subtriangular lobe, which is curved rather strongly ventrad; the lateral and ventral sides of the aperture are approximately transverse to the long axis of the neck and are nearly straight, but there appears to be a tendency for them to become slightly concave and for small ventro-lateral lobes to be developed—such lobes are very distinct in the other two known species of this genus. The test is ornamented by faint longitudinal and transverse lines, which give it a reticulate appearance. The septum of truncation is a normal nautiloid septum, but it is rather strongly convex apicad and, as it slopes orad from the venter, is distinctly inclined to the long axis of the conch. The rest of the septa are not well preserved in any of the typical mature specimens that have been figured, but apparently the dorsal part of the septum just orad of the septum of truncation curves strongly orad and somewhat ventrad so as to form a long deep dorsal saddle; this septum then curves abruptly dorsad and meets the dorsum only slightly apicad of the mid-length of the living chamber proper. The nature of the rest of the septa in the ventral half of the conch of this species is not known as Barrande failed to detect them, but they probably are not greatly different from those of *Glossoceras lindstroemi*, n. sp., discussed below. The five adoral sigmoidal septa are not complete centrally, and they separate from the preceding septum and then from each other in the adoral half of the specimens; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. All of the sutures of these septa appear to coalesce successively below the dorsum along the lateral sides of the conch; they probably are distinct along the ventral side of the conch, but Barrande's figures do not show them. Very little information is available in regard to the siphuncle of this species, but it is ventral in position and is small at its passage through the septum of truncation but appears to be expanded within the adjacent camera; it probably is not very different from that of *Glossoceras lindstroemi*, discussed below.

As mentioned above, Lindström (pp. 33-34, pl. 5, figs. 44-52) discovered a representative of this genus in the upper Middle Silurian of Gotland and studied and described it in his masterly way. He referred his specimens to "*Glossoceras gracile* var. *curta* Barrande" but recognized that they presented certain differences from that form, e.g., in the shape of the tongue-like lobe on the dorsal side of the aperture, and it now seems desirable to regard them as representing a distinct species; it is here proposed to call it *Glossoceras lindstroemi,* in honor of its discoverer. The known portion of its conch, the adoral or cyrtochoanitic part, is shorter than that of the genotype and consists of only four or five camerae of the phragmacone and the living chamber, but otherwise the two species are not greatly different, and our knowledge of the internal structure of this form will serve in lieu of that of the genotype. The first sigmoidal septum is complete and is essentially like that of the genotype described above; the rest of the adoral sigmoidal septa unite immediately dorsad of the siphuncle and then coalesce with the preceding septum; they become distinct from that septum again only in the adoral half of the specimens. The siphuncle of this portion of the conch is small at its passage through the septa, but its segments are greatly expanded transversely within the camerae, and the septal necks apparently are strongly recurved. The segment of the siphuncle between the septum of truncation and the first sigmoidal septum is subglobular in shape, but the other adoral segments are much shorter and are asymmetrically subnummuloidal.

As near as the writer has been able to tell from the literature, only three species of this genus are known, and all three are strikingly similar and are confined to the upper Middle Silurian. They are: *Glossoceras gracile* (Barrande) (the genotype) and *G. curtum* (Barrande)[24] of division "e2" of stage E (= Eβ of Kettner and Kodym) of the upper Middle Silurian of Bohemia, and *G. lindstroemi* Miller (named above and described by Lindström, 1890, pp. 33-34, pl. 5, figs. 44-52) of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland.

The small specimen from the oölitic limestone of division "e1" of stage E of the Middle Silurian of Bohemia, that Barrande (1877, p. 241) referred to *Glossoceras gracile,* only because of its slender

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[24] This form was described by Barrande as a variety of *Glossoceras gracile,* but it is here regarded as a distinct species.

form and the reticulate ornamentation of its conch, is so incomplete and so inadequately described that it is not now possible to place it generically; the adoral part of the specimen is not preserved, and the only septum that is discernible from Barrande's figures is the septum of truncation. Narrow conchs and reticulate surface ornamentation are now known to occur in several genera of the mixochoanitic cephalopods.

The specimen from the upper Middle Silurian (Chicotte) of Anticosti Island that Billings (1866, p. 60) described as *Glossoceras desideratum* has recently been redescribed and figured by Foerste (1928, pp. 261-262, pl. 40, fig. 2) as "*Orthoceras desideratum* (Billings)." It bears so little resemblance to typical *Glossoceras,* that one can not help but wonder why Billings referred it to this genus. Also, it is extremely doubtful if the single specimen from an unknown horizon in southeastern Poland (Łanowce) that Siemiradzki[25] described and figured as *Glossoceras carinatum* (the specific name is ascribed to Alth, who apparently used it in unpublished manuscript) actually represents this genus. That specimen is a small fragment which apparently was interpreted as representing the extreme adoral end of the living chamber, and the only published description of it is so incomplete as to be of little value.

Lindström has suggested (p. 33) that this genus can be differentiated from typical *Ascoceras* by the fact that the adoral dorsal portion of its phragmacone continues to increase in dorso-ventral thickness adorally, whereas in *Ascoceras* the adoral segments of the phragmacone are relatively small. This is true in the examples cited by Lindström, but there are so many exceptions to it, that the generalization is of little value. As a matter of fact, the conchs of members of this genus are very similar to those of some of the representatives of *Ascoceras* and can be distinguished from them only by their lobed apertures. The genus can be differentiated from other similar genera by the criteria mentioned at the close of the discussion of the genus *Ascoceras*.

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[25] Siemiradzki, Jos. von, Die paläozoischen Gebilde Podoliens: Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, vol. 18, pp. 203, 227, pl. 18 (4), figs. 7a, b, c, 1905.

Genus CHOANOCERAS Lindström 1890

[= *Choaniceras* Lindström 1888, *nomen nudum*][26]

Plate IX, Figs. 1-9

This genus was established by Lindström to include a unique species, *Choanoceras mutabile* Lindström of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland, and as far as the writer has been able to learn no other representative of it has been recorded since.[27] The genotype has been exceedingly well described by Lindström (pp. 35-37), but in as much as his monograph is not readily available to many paleontologists, the following concise description may prove of interest.

The conch is long and narrow and, being circular in cross section and only very gradually expanded orad, is essentially cylindrical in shape, but it is gently curved exogastrically. The earlier stages of the phragmacone are not known, and apparently they were broken off during the life of the individual; the conch of mature specimens consists of the adoral five camerae of the phragmacone and the living chamber. In these specimens the living chamber occupies at least nine-tenths of the remaining portion of the conch. The extreme adoral portion of the conch has never been observed, but as none of the known representatives is contracted adorally, the aperture probably was not constricted and was circular in outline. The surface of the test is marked by fine sinuous longitudinal lines and that of some internal molds by "microscopically small elevated points," which Lindström regarded as "belonging to an interior stratum of the shell."

The sutures are all parallel and nearly straight but are slightly inclined to the long axis of the conch; they slope orad from the venter. The septa are asymmetrically subconical in shape, and in mature specimens the adoral three are not complete as they unite and then coalesce with the preceding septum slightly ventrad of the siphuncle and become distinct from it again only in the extreme ventral part of the conch; this leaves a large elliptical lacuna in the ventral half of each septum, that is comparable to the much larger lacuna in the dorsal portion of the adoral septa of the ascoceratoids. In immature specimens only the adoral three cam-

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[26] Lindström, G., List of fossil faunas of Sweden, p. 7. [Not seen by the writer]

[27] Hyatt (1900, p. 515) and Broili (1924, p. 524) list this genus as occurring in both the Ordovician and the Silurian, but the writer has not been able to locate the basis for this statement.

erae of the phragmacone are retained and all of the septa are complete, but as the individuals near maturity, the number of camerae that are retained is increased, the septa become more strongly asymmetrical and the distance between them is decreased, and the adoral septa coalesce in the ventral half of the conch as explained above.

The siphuncle is small at its passage through the septa but the septal necks are strongly recurved and the segments of the siphuncle are greatly expanded transversely within the camerae. The shape of the connecting rings varies with the stage of growth of the individual; in the smallest specimen known they are subcylindrical, but in somewhat larger specimens they are relatively shorter and are subspherical, whereas in mature specimens they are asymmetrically subnummuloidal.

It is perhaps very significant that in mature specimens a peculiar deposit, called a "spur" by Lindström, is formed on the inside of the septal necks. This deposit nearly closes the septal aperture, and Lindström detected a small conical plug that sealed the remaining opening in the septum of truncation.

The relationship of this genus to the genera described above is more or less of an open problem. The variation in the shape of the siphuncular segments in the different parts of the phragmacone, the coalescing of the adoral septa, and the truncation of the earlier stages of the phragmacone, all indicate a relationship to the ascoceratoids. However, that relationship can not be very close for the siphuncle of this genus is essentially central in position, the change in the shape of its segments is gradual, as far as is now known all of the septal necks are strongly recurved, the septa coalesce on the ventral side of the conch instead of on the dorsal (or, as is possible but very improbable, the conch is curved endogastrically rather than exogastrically), the septa are much more strongly convex and do not form long deep dorsal saddles, and the adoral part of the conch is not contracted so that the aperture apparently remained wide open throughout the life of the individual. It is probable that the shape of the aperture has been over emphasized in the classification of the nautiloids, for it probably depends somewhat upon feeding habits, i.e., those forms with strongly constricted apertures must have fed on microscopic food; nevertheless, the fact that in this genus the aperture is so markedly different from those of all of the other forms discussed above, serves to emphasize lack of close relationship.

These facts, taken together, have led the writer to the conclusion that this genus must represent a stock that differentiated from the main stock of the Mixochanites early in the Ordovician, and that we have not discovered earlier representatives of the group as yet. It is therefore believed that *Choanoceras* should be regarded as an outlying member of the Mixochoanites, but it certainly should not be placed in the same family with any of the other known forms.

THE EVOLUTION OF THE MIXOCHOANITES

With one or two possible exceptions, the genera discussed above constitute a group of nautiloids that are closely related and are quite distinct from all of the other multitudinous forms known. The most significant feature that they share in common, and is not known to occur in any of the other groups of nautiloids, is the marked change in the nature of their siphuncle as they near maturity, i.e., a change from an orthochoanitic to a cyrtochoanitic structure. This, taken together with such other abnormal features as the unusual shape of their conchs, the universal truncation of the earlier stages of their phragmacones, and the peculiar shape and the coalescing of their adoral septa, makes it obvious that these forms constitute a distinct group, for which the name Mixochoanites of Hyatt is particularly applicable.

This group apparently originated early in the Ordovician[28] and can be definitely recognized by the middle of that period in *Probillingsites*. That genus obviously developed out of an *Oncoceras*-like form, but the writer has not been able to locate a definite ancestor of it. The available evidence seems to indicate that *Probillingsites*, or its progenitor, gave rise to two stocks which can be differentiated by the presence or absence of a so-called "basal" septum. These stocks became distinct at least by Upper Ordovician times and developed along closely parallel lines to the close of the Middle Silurian. In the upper Middle Silurian both apparently reached a climax, for they suddenly branched out into a variety of forms and then became extinct. What appears to be the culmination of a third stock is to be seen in *Choanoceras* of the upper Middle Silurian, but unfortunately the earlier stages of that stock are not known. Apparently it differentiated from the main stock of the Mixochoanites early in the Ordovician, and we have not found any but its ultimate stage as yet.

The general scheme of the evolution of this group as conceived by the writer is obvious from the accompanying diagram, and few

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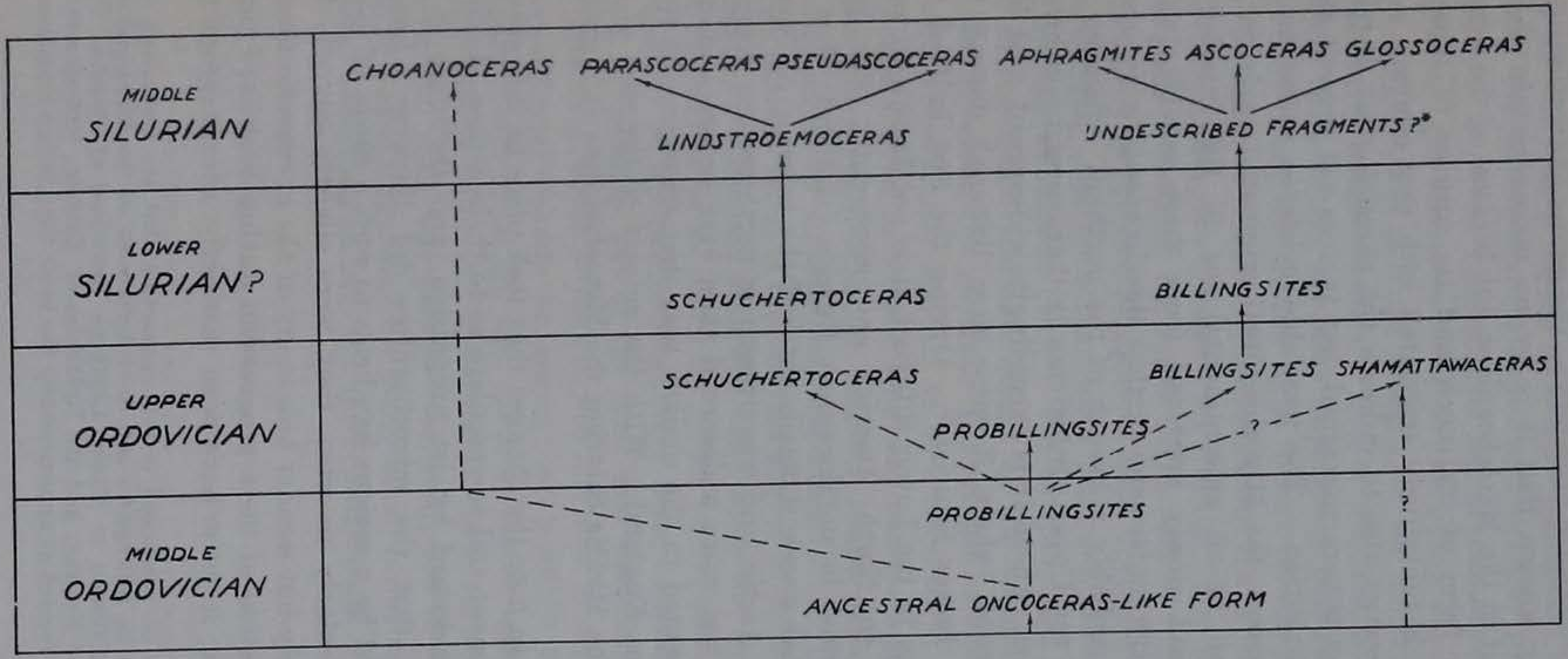
[28] The specimens from the Ozarkian (Oneota dolomite) of Dresbach, Minnesota, that were described by F. W. Sardeson (Minnesota Acad. Nat. Sci. Bull., vol. 4, no. 1, p. 102, 1896) under the name "Ascoceras gibberosum" are stated by Foerste (1924, p. 217) on the authority of E. O. Ulrich to represent "a new genus of *Chiton*, related to *Priscochiton*, now under investigation."



PHYLOGENIC TABLE OF THE MIXOCHOANITES

* Indeterminable fragments of ascoceratoids in the oölite of Bursvik and the limestone of östergarn, Gotland, (both formations are of lower Middle Silurian age) may represent an intermediate stage between *Billingsites* of the Upper Ordovician and probably the Lower Silurian and *Ascoceras* s. s., *Aphragmites*, and *Glossoceras* of the upper Middle Silurian—no description of them has been published.

supplementary remarks are necessary. The genus *Shamattawaceras* is so incompletely known that it is by no means certain that it should be included in the Mixochoanites, but because of the general similarity of the form of its conch and its sutures to those of *Probillingsites*, it is tentatively associated with that genus.

This diagram serves also to indicate the chronological distribution of the various genera concerned, but it does not present their geographical distribution. The available evidence seems to indicate that this group, the Mixochoanites, originated early in the Middle Ordovician in an epicontinental sea in the interior of North America and slowly migrated from there northeastward, where it apparently underwent further development in an arctic or subarctic sea, probably a branch of the northern Atlantic. In the latter part of the Upper Ordovician it then spread southward into North America, where it is exceedingly widespread, and into northwestern Europe, where it may have lingered during the early part of the Lower Silurian[29]. During the first half of the Middle Silurian, as in the Lower Silurian, it is not known to have been represented in North America and apparently was only sparingly represented in northwestern Europe (Gotland), but in the last half of that epoch it again entered the interior of North America from the Arctic, and was present in northwestern Europe as well, where it was more widespread than ever before and was abundantly represented in the shallow seas that transgressed Gotland, Bohemia, and England. With the retreat of the seas at or near the close of the Middle Silurian the Mixochoanites as a group became extinct.

It is interesting to note the changes that took place in this group during its development and to speculate as to their causes. Living nautiloids swim backward by jet propulsion, and therefore it is logical to assume that the mixochoanites did likewise. Long, slender shells would be a serious handicap to such a mode of locomotion, and particularly so when they were slightly curved—in fact one can not help but wonder how many of the cyrtoconic forms controlled the direction of their progression during backward propulsion. Therefore, it must have been distinctly advantageous to

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[29] It should perhaps be mentioned in this connection that the occurrence of such transitional types as *Billingsites* and *Schuchertoceras* in the Richmond of North America, the Kallholn or Upper Leptaena limestone of Sweden, the Gastropod limestone of Norway, and the Lyckholm of Estonia, indicates that those deposits were all formed at approximately the same time in one continuous sea.

break off the earlier stages of the phragmacone and thus remove much of the impediment to rapid and straight progression. Such truncation, however, necessitated the development of a few large camerae or gas chambers next to the living chamber to serve as buoys, and this will perhaps account for the globular form assumed by the early mixochoanites. Utopia was not attained, however, by these early forms, for they apparently had two serious handicaps: first, when the animal came to rest its conch must naturally have assumed a vertical position with the aperture down (cf. modern *Spirula*); and, second, its globular form must have retarded its passage through the water. The first of these handicaps was surmounted by the development of long, deep dorsal saddles in the adoral septa (the ones that were retained after truncation), so that the phragmacone (buoy) was extended all along the dorsal part of the conch and the weight of the animal's body was distributed all along the ventral. The second handicap was overcome by what superficially appears to be a reversal in evolution in that the conch tended to become long and narrow again, but this time it assumed a spindle-like or fusiform shape, which is particularly advantageous for subaqueous locomotion.

The curious thing is that in this group, as in many other groups of animals, extinction followed close upon the heels of perfection, and the writer is as much at a loss to explain this phenomenon adequately as his predecessors have been. Possibly it was due to a lack of weeding out of the unfit and therefore a weakening of the race as a whole so that it was not able to cope with some new environmental change or enemy; or possibly the group simply perished from racial old age. It is of course true that at the close of the Middle Silurian the habitat of these forms, the shallow epicontinental seas, was greatly restricted, but it is hardly probable that it was extinguished for many other forms requiring a similar habitat continued on into the succeeding epoch.

THE CLASSIFICATION OF THE MIXOCHOANITES

The characters which differentiate this group from the rest of the nautiloids are given above, and in the writer's opinion the group is quite as distinct as it was regarded by Barrande and Hyatt and should therefore be considered as representing one of the major divisions of the order Nautiloidea and be accorded the rank of a suborder. Hyatt, the only paleontologist who has so far attempted to subdivide the group into units larger than genera, recognized two families, but in as much as one of them included only *Mesoceras,* which apparently should be excluded from the suborder, and *Billingsites,* which is in the direct line of the evolution of *Ascoceras,* the type of the other family, his subdivisions are no longer tenable.

If the evolution postulated above is correct, three logical subdivisions of this group should be recognized. The two main stocks apparently differentiated from *Probillingsites* or its progenitor before the Upper Ordovician and can be followed almost continuously to the close of the Middle Silurian, when both became extinct. One of these, which is characterized by the absence of a so-called basal septum and, in some cases, by the possession of a relatively large number of sigmoidal septa (in one form as many as twelve) in the adoral part of the conch, can be definitely recognized in *Billingsites* and followed through to its culmination in *Ascoceras, Aphragmites,* and *Glossoceras.* The other stock, which is characterized by the possession of a basal septum, or vestiges of it[30], and a relatively small number of sigmoidal septa (never more than four or five) in the adoral part of the conch, can be recognized in *Schuchertoceras* and followed through *Lindstroemoceras* to its culmination in *Parascoceras* and *Pseudascoceras.* The third stock, which apparently culminated in *Choanoceras,* probably originated early in the Ordovician, but at present we know it from only its ultimate stage. This stock can be differentiated from the other two by the fact that its siphuncle is essentially central in position, the change in the shape of its siphuncular segments is

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[30] In at least two representatives of this family, *Schuchertoceras* and *Pseudascoceras,* the first septum formed orad of the septum of truncation apparently was resorbed before the succeeding septum was secreted.

gradual, all of its septal necks (as far as is now known) are strongly recurved, its septa coalesce on the ventral (rather than the dorsal) side of its conch and do not form long, deep dorsal saddles, and the adoral part of its conch is not contracted and its aperture apparently was wide open throughout the life of the individual.

The writer would therefore recognize three families of the Mixochoanites; one of these has been aptly named Ascoceratidae by Barrande, and it is here proposed to call the second Schuchertoceratidae and third Choanoceratidae. All of the genera known fall logically into these three families, with the possible exception of *Probillingsites* and, along with it, *Shamattawaceras*. Both of these genera are so incompletely known that it is not now possible to determine whether they should be placed in the Ascoceratidae or the Schuchertoceratidae, or whether *Probillingsites* should be regarded as the ancestor of both of those groups. In view of the equivocal nature of the available evidence, the writer has thought it best to place *Probillingsites* tentatively in the Ascoceratidae, as that group was far more abundant than the other and apparently should be regarded as constituting the main stem of the Mixochoanites; the other stocks then should be considered offshoots of it. *Shamattawaceras* is also tentatively assigned to the Ascoceratidae as apparently it should be associated with *Probillingsites*.

SUMMARY

To summarize the above statements, it can be stated that the Mixochoanites, which are confined to the Ordovician and Silurian of central and northeastern North America and northwestern Europe, constitute a natural group of nautiloids that is distinct enough to deserve the rank of a separate suborder; that certain of the genera, viz., *Volborthella, Ophidioceras,* and *Mesoceras,* that have been included in that group have little or no relation to it and should be excluded from it; and that the number of subdivisions, both genera and families, of the group that have been recognized previously is not as large as the diversity of its forms justifies. The following classification of the group is therefore proposed:

Suborder MIXOCHOANITES Hyatt

- Family ASCOCERATIDAE Barrande
    - Genus *Ascoceras* Barrande
    - Genus *Aphragmites* Barrande
    - Genus *Glossoceras* Barrande
    - Genus *Billingsites* Hyatt
    - Genus *Probillingistes* Foerste
    - Genus *Shamattawaceras* Foerste and Savage

- Family SCHUCHERTOCERATIDAE Miller, n. fam.
    - Genus *Pseudascoceras* Miller, n. gen.
    - Genus *Parascoceras* Miller, n. gen.
    - Genus *Lindstroemoceras* Miller, n. gen.
    - Genus *Schuchertoceras* Miller, n. gen.

- Family CHOANOCERATIDAE Miller, n. fam.
    - Genus *Choanoceras* Lindström

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PLATE I

PAGE

Figs. 1-14. *Volborthella tenuis* Schmidt 10

All specimens figured are from the Lower Cambrian of Estonia. Figures 1-11 are after Karpinsky, and figures 12-14 are after Schindewolf.

1. Upper surface of a slab of sandstone showing local abundance of this small gregarious form along a bedding plane, x 3.

2, 3. Lateral and dorsal or ventral views showing shape of conch, x 16.

4-9. Apertural views of six specimens (internal molds) illustrating varied nature of aperture, x 20.

10, 11, Cross-sectional views of two specimens showing "siphuncle", x 19.

12. Diagrammatic longitudinal section showing septa and "septal necks," x 15.

13, 14. Retouched photographs of two of the thin-sections on which the preceding diagram was based, x 8.

PLATE I

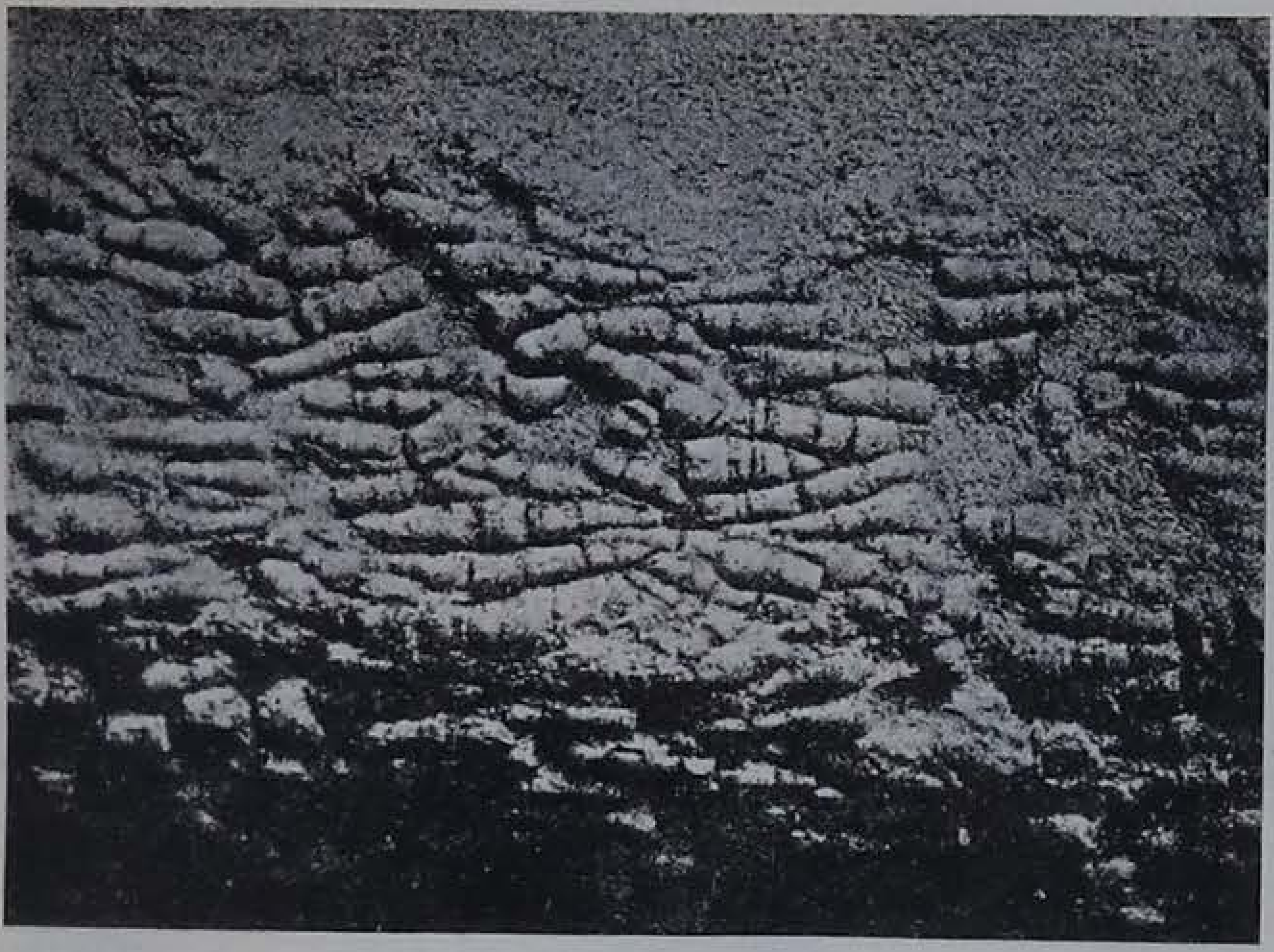
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PLATE II

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Figs. 1, 2. *Ophioceras nakholmensis* (Kjerulf) 15

Lateral and ventral views of the holotype from the Ordovician of Nakholmen, Norway, x 1. After Kjerulf.

Figs. 3-7. *Euophioceras simplex* (Barrande) 17

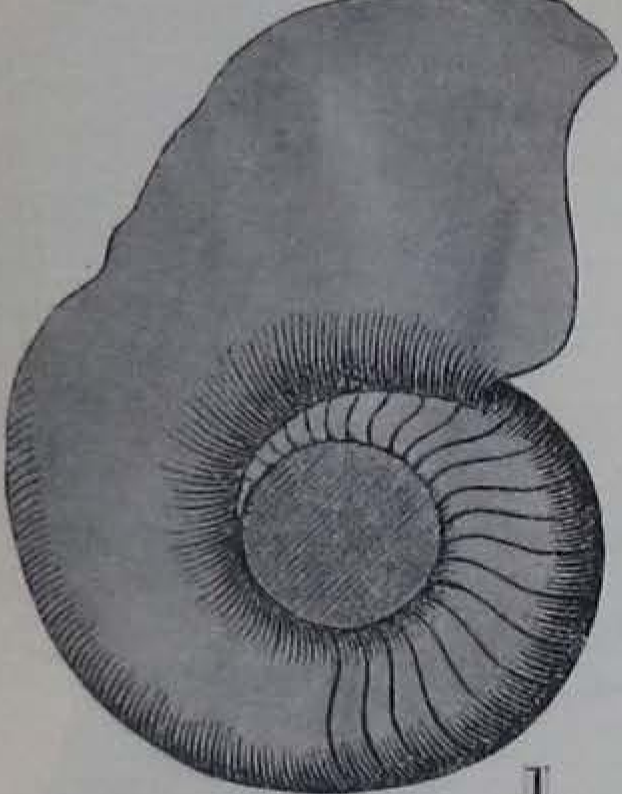
3-6. Lateral, cross-sectional, apertural, and dorsal views of a complete specimen from the Middle Silurian of Bohemia, x 2. After Barrande.

7. Longitudinal section of another specimen, also from the Middle Silurian of Bohemia, x 1. After Barrande.

Figs. 8-12. *Mesoceras bohemicum* Barrande 19

Apertural, septal, lateral, and dorsal views of the holotype from the Middle Silurian of Bohemia, x 1; and ventral view of the same slightly enlarged. After Barrande.

PLATE II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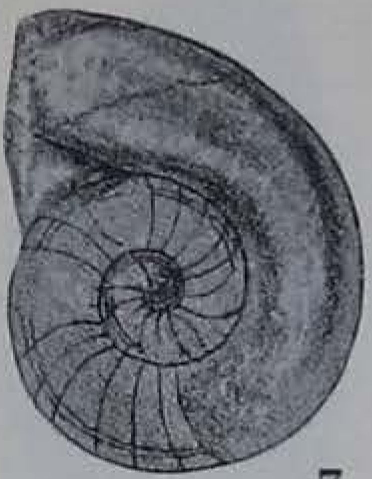
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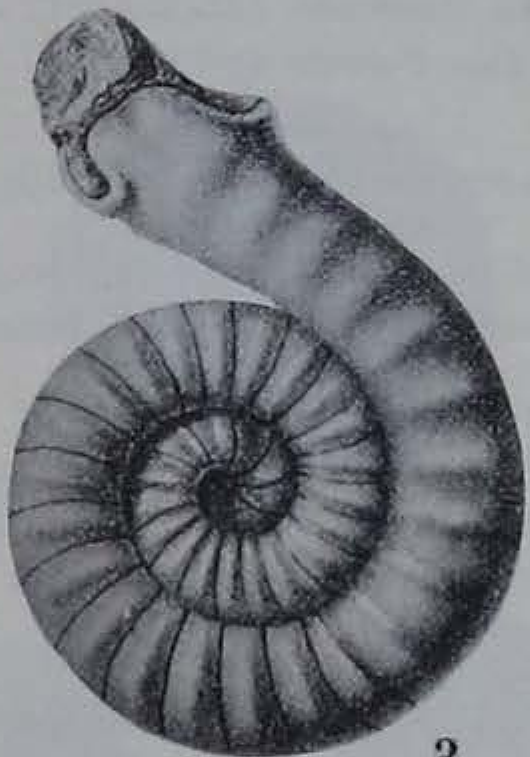
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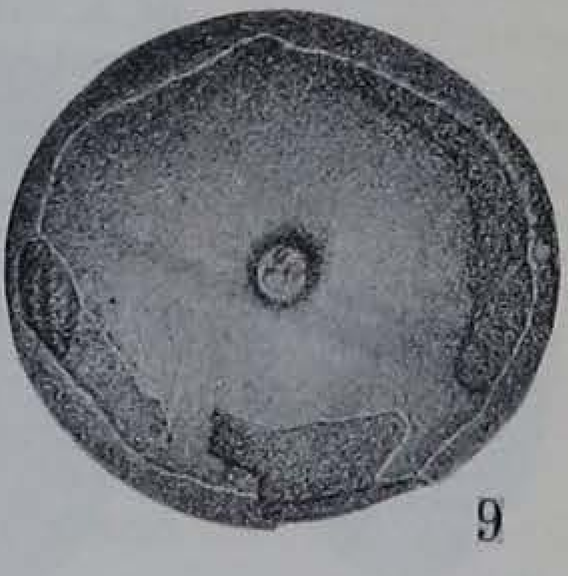
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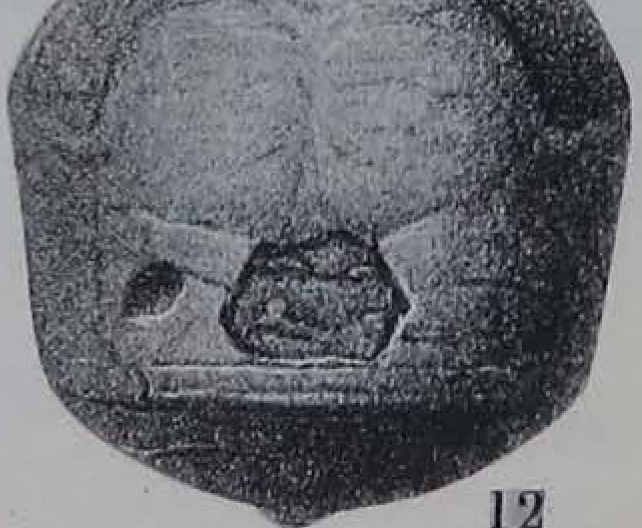
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PLATE III

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Figs. 1-3. *Shamattawaceras ascoceroides* Foerste and Savage 22

Ventral, lateral, and dorsal views of the holotype from the Shamattawa limestone (Richmond) of northeastern Manitoba, x 1. After Foerste and Savage.

Figs. 4-9. *Schuchertoceras anticostiense* (Billings) 28

4, 5. Dorsal and lateral views of the neoholotype from the Ellis Bay (Gamachian) of Anticosti Island, x 1. After Foerste.

6-8. Apical, lateral, and dorsal views of a specimen (Yale Peabody Museum, 3807b) showing the impression of the septum of truncation, from Zone 7 of the Ellis Bay (Gamachian) of a cliff between Bear Cliff and Cape Eagle, Anticosti Island, x 1.

9. Longitudinal section of same specimen as the preceding showing the septa and the siphuncle, x 1.

Figs. 10-13. *Probillingsites* Foerste 20

10, 11. Lateral and ventral views of the holotype of *P. welleri* Foerste, the genotype, probably from the Galena of Wisconsin, x 1. After Foerste.

12. Lateral view of the holotype of *P. manitoulinensis* (Foerste) from the Meaford member of the Richmond of the eastern margin of Manitoulin Island, x 1. After Foerste.

13. Lateral view of the holotype of *P. primus* (Fritz) from the Upper Cobourg member of the Utica group, east of Collingwood, Ontario, x 1. After Fritz.


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PLATE IV

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Figs. 1-6. *Billingsites canadensis* (Billings) 24

1. Lateral view of the holotype from the English Head (Richmond) of Anticosti Island, x 1. After Foerste.

2. Lateral view of a typical example showing the aperture, from the English Head (Richmond) of Anticosti Island, x 1. After Foerste.

3-5. Dorsal, lateral, and apical views of a specimen (Yale Peabody Museum, 3809) showing the impression of the septum of truncation and the large, well developed siphuncle at the apical end, from Zone 4 of the English Head (Richmond) of Charleton Point, Anticosti Island, x 1.

6. Longitudinal median section of same specimen as the preceding showing the septa and the siphuncle, x 1.

PLATE IV


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PLATE V

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Figs. 1-6. *Lindstroemoceras* Miller, n. gen. 32

All specimens figured are from the lower Middle Silurian of Gotland, and all figures are after Lindström.

1-4. Dorsal (x 1), lateral (x 1½), apical (x 1½) and longitudinal-sectional (x 2) views of a cotype of *L. dolium* (Lindström), the genotype.

5. Lateral view of the second cotype of *L. dolium* (Lindström), x 1.

6. Lateral view of a cotype of *L. cochleatum* (Lindström), x 1.

Figs. 7-21. *Pseudascoceras decipiens* (Lindström) 37

All specimens figured are from the upper Middle Silurian of Gotland, and all figures are after Lindström.

7-10. Lateral, ventral, cross-sectional (diagrammatic) and longitudinal-sectional views of a typical representative, x 1.

11. Enlargement of apical end of same specimen as the preceding to show the septa, x 3.

12. Internal mold showing sutures, x 1.

13, 14. Longitudinal section of a senile individual showing four adventitious septa, x 1, and an enlargement of the apical part of the same specimen, x 10.

15. Immature individual retaining part of the orthochoanitic stage of the conch and showing only one sigmoidal septum, x 1.

16, 17. Longitudinal section of same specimen as the preceding, x 1, and an enlargement of its apical part to show the siphuncle, x 6.

18, 19. Fragment of an immature representative and longitudinal section of the same showing the two parts of the conch connected and proving that at least much of the adoral part of the conch was formed before the sigmoidal septa were secreted, x 1.

20. Fragment of the orthochoanitic part of the conch showing the apex, x 1.

21. Restoration showing longitudinal section of the entire conch, x 1.

PLATE V

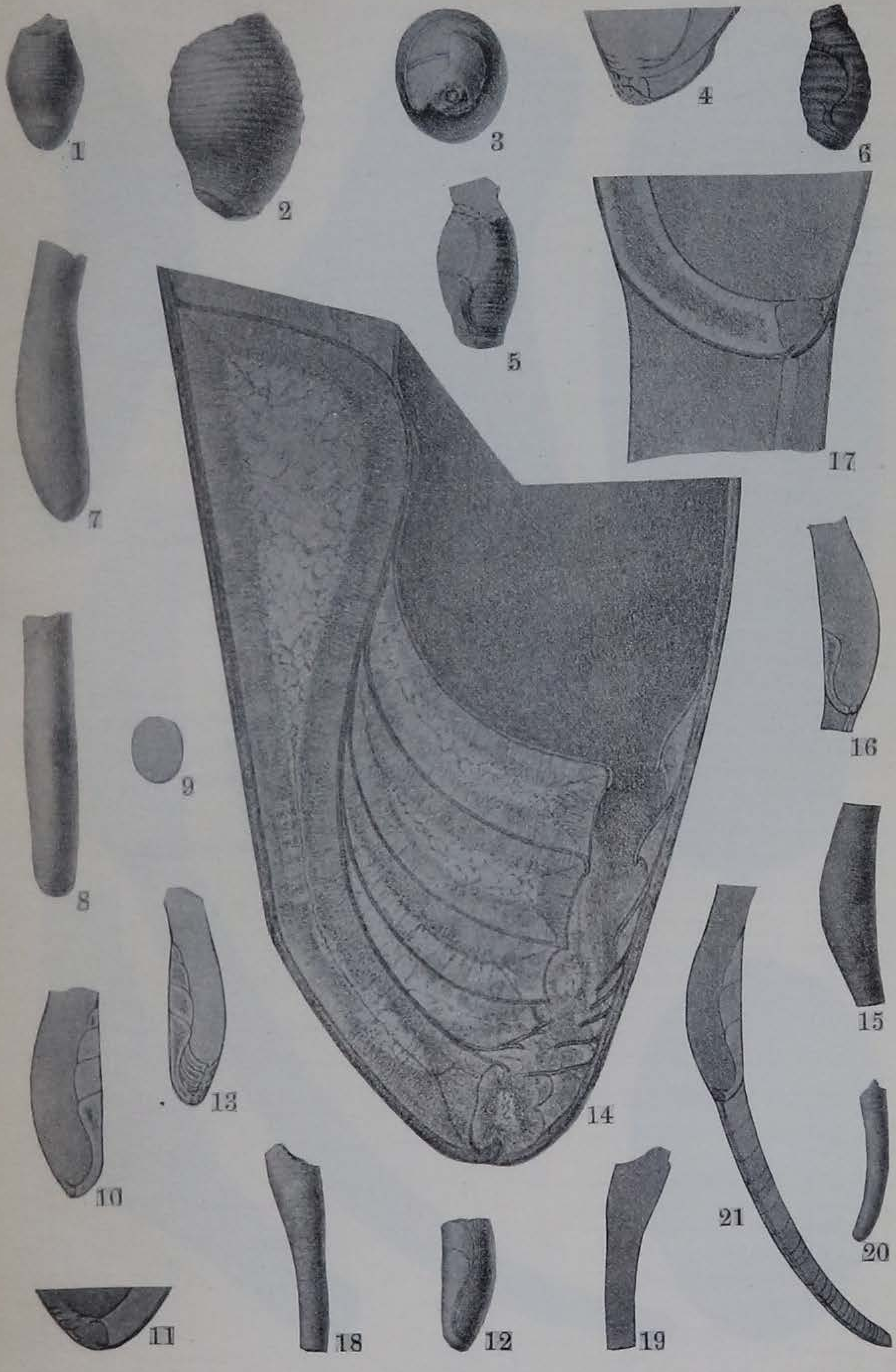

PLATE VI

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Figs. 1-3. *Ascoceras bohemicum* Barrande 41

Lateral, dorsal, and apical views of a typical, mature specimen from the upper Middle Silurian of Bohemia, x 1. The adoral neck has been restored in the lateral view. After Barrande.

Figs. 4-6. *Ascoceras lagena* Lindström 41

4, 5. Lateral and longitudinal-sectional views of a cotype from the upper Middle Silurian of Gotland, showing the two parts of the conch connected, i.e., before truncation, x 1. After Lindström.

6. Restoration showing longitudinal section of the entire conch, x 1. After Lindström.

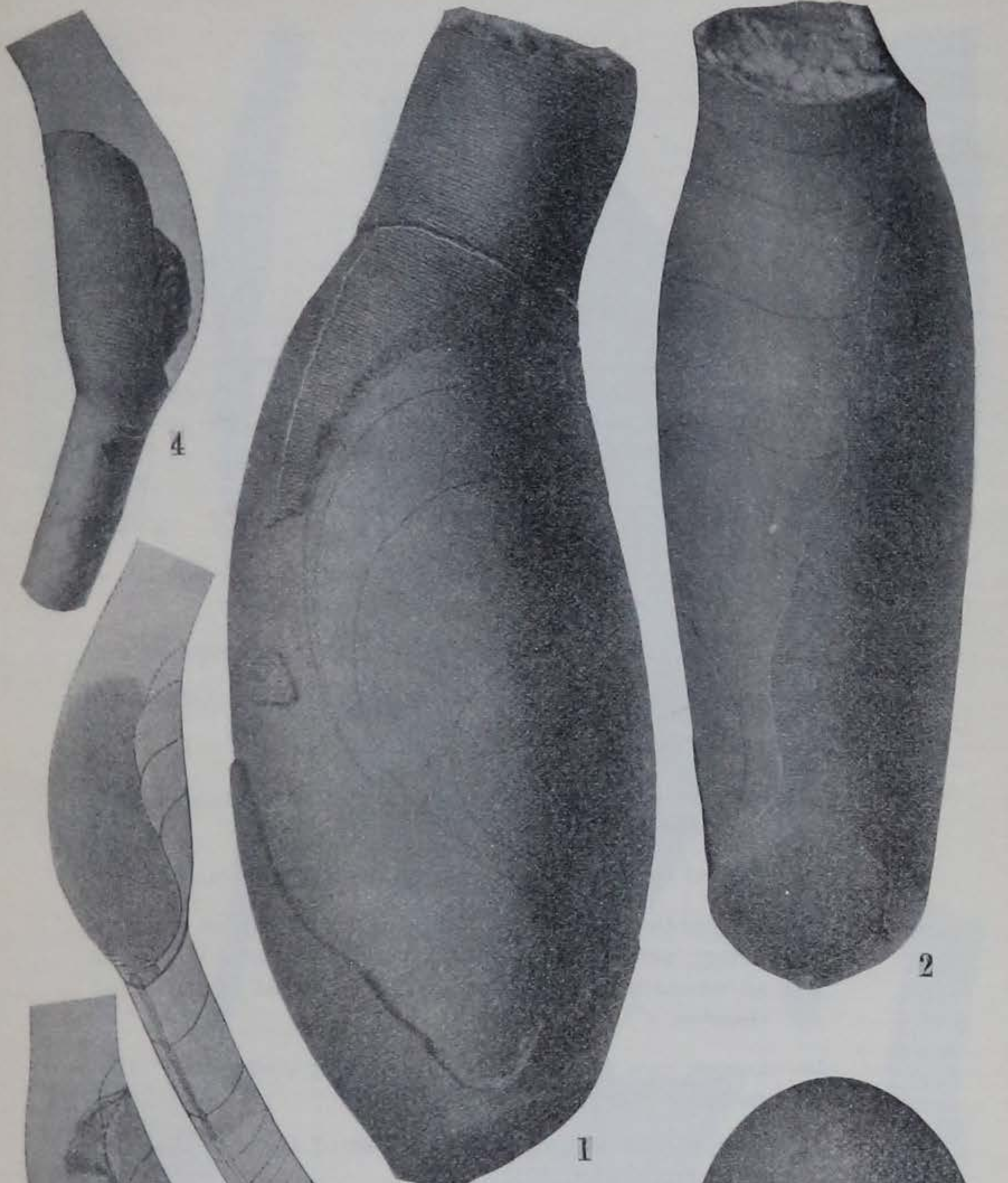
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PLATE VII

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Figs. 1, 2. *Ascoceras bohemicum* Barrande 41

Longitudinal section (x 1) of a mature specimen from the upper Middle Silurian of Bohemia, and an enlargement of the apical end of the same to show the nature of the siphuncle, x 1½. After Barrande.

Figs. 3-12. *Parascoceras fistula* (Lindström) 34

All specimens figured are from the upper Middle Silurian of Gotland, and all figures are after Lindström.

3. Lateral view of a specimen showing surface sculpture, x 2.

4. Longitudinal section of same specimen as the preceding, x 1.

5, 6. Dorsal and apical views of a similar specimen, x 1.

7. Longitudinal section of a typical, mature individual showing shape of segments of siphuncle, x 3.

8. Lateral view of an internal mold showing sutures, x 2.

9. Longitudinal section of the same individual as the preceding, which is in a senile stage of development and shows an adventitious septum in the posterior end of the living chamber, x 2.

10. Lateral view of a specimen representing most of the orthochoanitic part of the conch, x 2.

11. Longitudinal section of a fragment of the orthochoanitic part of the conch, x 1.

12. Restoration showing longitudinal section of the entire conch, x 1.

Plate VII


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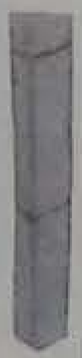
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PLATE VIII

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Figs. 1-9. *Aphragmites buchi* (Barrande) 45

All specimens figured are from the upper Middle Silurian of Bohemia, and all figures are after Barrande.

1-3. Lateral, dorsal, and cross-sectional views of a mature specimen retaining part of the test along the dorsum, x. 1.

4. Lateral view of an internal mold showing the sutures, x 1.

5. Dorsal view of another internal mold showing sutures, x 1.

6-9. Dorsal, lateral, cross-sectional, and apical views of the same specimen as the preceding with the dorsal part of the phragmacone removed, x 1.

Figs. 10, 11. *Ascoceras townsendi* Whiteaves 41

Apical and lateral views of the holotype from the Guelph of Durham, Ontario, x 2. After Whiteaves.

Figs. 12-25. *Glossoceras* Barrande 49

12-17. Dorsal, lateral, ventral, apertural, apical, and cross-sectional views of a typical, mature specimen of *G. gracile* Barrande of the upper Middle Silurian of Bohemia, x 1. After Barrande.

18-20. Dorsal, lateral, and cross-sectional views of another mature specimen of *G. gracile* Barrande, from which the dorsal portion of the phragmacone has been removed, x 1. After Barrande.

21-25. Ventral, lateral, apertural, and longitudinal-sectional views, x 1, of *G. lindstroemi* Miller, n. sp., of the upper Middle Silurian of Gotland; and an enlargement of the apical portion of the last to show the structure of the siphuncle, x 6. After Lindström.

PLATE VIII

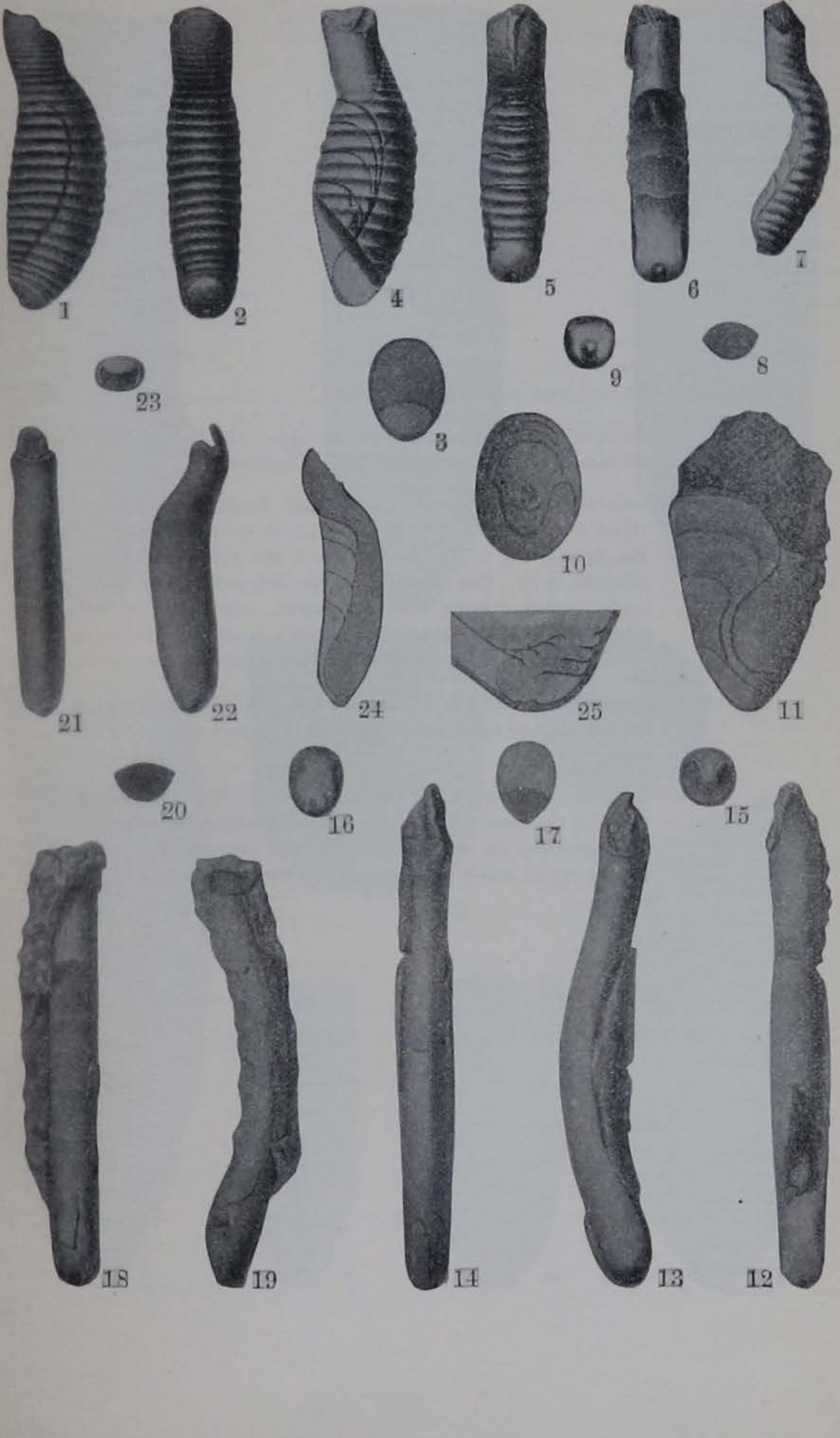

PLATE IX

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Figs. 1-9. *Choanoceras mutabile* Lindström 53

All specimens figured are from the upper Middle Silurian of Gotland, and all figures are after Lindström.

1-6. Lateral, dorsal, ventral, apical, and longitudinal-sectional views of a mature specimen, x 1; and an enlargement of the apical end of the last to show the nature of the siphuncle, x 3. The deposits on the interior of the septal necks, called ''spurs'' by Lindström, are shown on the adapical septa of this specimen, and a small plug is shown closing the remaining aperture in the septum of truncation.

7, 8. Longitudinal sections of immature representatives showing cylindrical and spherical connecting rings and four complete septa, x 1.

9. Longitudinal section of an individual in late adolescence showing the change in the shape of the siphuncular segments from globular to subnummuloidal, and showing five septa, the adoral of which is incomplete in the ventral part of the conch.

PLATE IX


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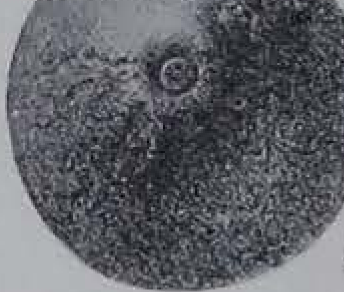
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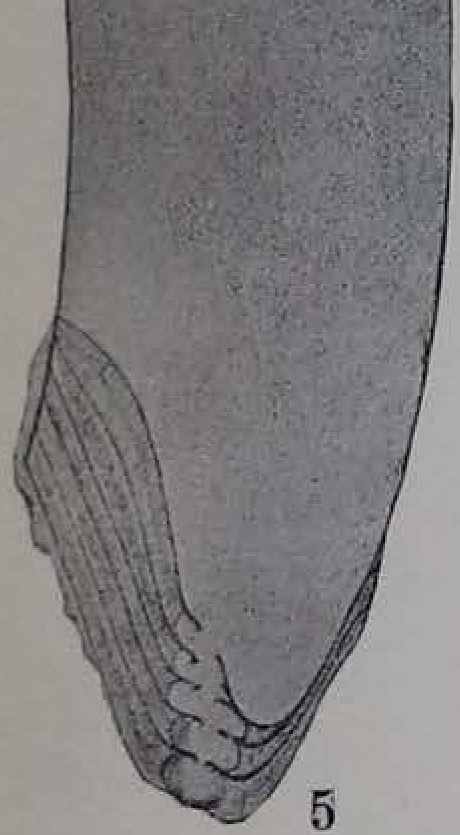
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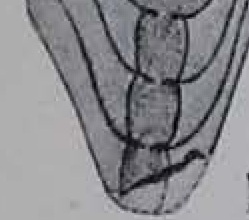
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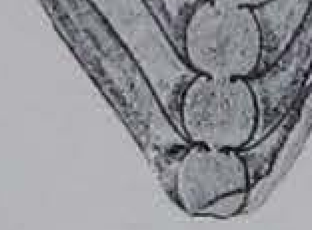
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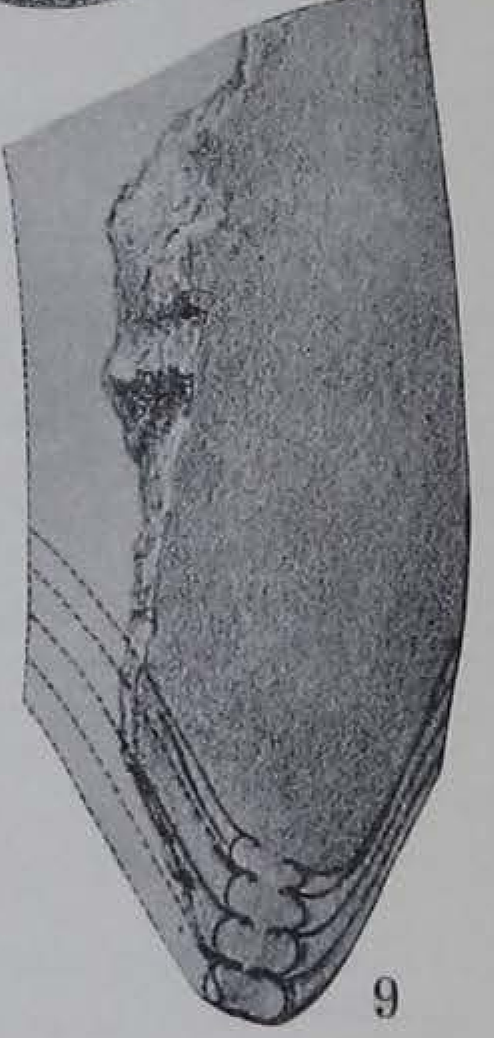
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