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A NEW BELEMNOID FROM THE TRIASSIC OF NEVADA

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ABSTRACT. A belemnoid from the Norian Gabbs formation of Nevada shows the external characteristics of the genus *Atractites* Boehm but contains a holochoanitic siphuncle composed of invaginated funnels (septal necks?) each of which extends through slightly more than two chambers. The name *Choanoteuthis mulleri* is proposed.

INTRODUCTION

IN the course of his studies on the Triassic of Nevada, Dr. Siemon Muller collected a belemnoid in the Norian Gabbs formation of the Gabbs Valley Range which, on external characters, resembled *Atractites* Boehm. This genus, as Flower (1944) has pointed out, has been used as a catch-all for early Mesozoic belemnoids with straight, axially located conchs[1] and smooth rostra. Thin-sections of the specimen revealed a type of siphuncular structure which differs markedly from any heretofore recorded for cephalopods of any sort, though somewhat resembling that of the holochoanitic nautiloids and of the Jurassic belemnoid *Megateuthis quinquesulcatus* de Blainville. Although the specimen at hand is only a fragment of rostrum and conch from the mid-alveolar region, the character of the siphuncle is so distinctive and of such potential significance to an understanding of belemnoid relationships that it is proposed to make it the basis of a new genus.

PHYLUM MOLLUSCA

CLASS CEPHALOPODA

Subclass Dibranchiata

Order Belemnoidea

Genus *Choanoteuthis*, n.g.

Description.—This genus is established for dibranchiate cephalopods which possess smooth, calcareous rostra of radiating fibers or prisms, slender conchs which are axially located (rather than excentric), fairly long chambers, and straight, slender, ventral siphuncles of holochoanitic structure; the siphuncle is composed of long, invaginated, retrosiphonate funnels, each of which extends through two or more preceding

[1] The term *conch* is here used collectively for the phragmocone, conotheca, and proostracum. It thus includes the entire skeleton except the rostrum.

chambers. These funnels are calcareous and comparatively thick, appearing to be greatly extended septal necks. However, the material at hand is not sufficiently well preserved to permit a definite conclusion as to whether they are septal necks throughout, or whether they are in part composed of thick, calcareous connecting rings of the type encountered among holochoanitic nautiloids (Flower, 1947).

Discussion.—Belemnoids possessing long, straight, axially located phragmocones and smooth, calcareous rostra have in the past been referred to *Atractites* Boehm. As there exists uncertainty about the genotype of *Atractites*, Flower (1944) has urged the transfer of most species from this into a newly established genus, *Ausseites* Flower, based on *Atractites ausseanus* Mojsisovics, and has split off from this group the genus *Metabelemnites* Flower, based on *Atractites philippii* Hyatt and Smith from the Upper Triassic of California.

Choanoteuthis resembles *Ausseites* and differs from *Metabelemnites* in its small angle of expansion, its comparatively long chambers, and in possessing inflated rather than cylindrical siphuncular segments. The microstructure of the siphuncle of *Metabelemnites* is not known. *Choanoteuthis* differs from *Ausseites* in the structure of the siphuncle: the genotype of the latter shows an essentially orthochoanitic development of short septal necks and long, delicate connecting rings which are slightly inflated. *Choanoteuthis* is thus readily differentiated from the other genera of belemnoids characterized by straight, axially located conchs and smooth rostra. Its siphuncular structure appears to be more closely related to (though not identical with) that of *Megateuthis quinquesulcatus* de Blainville from the Jurassic, described by Christensen (1925). In this form, the septum is extended into a funnel (it is not clear whether this is a septal neck, or connecting ring, or both) which extends apicad for a distance of one and one-half

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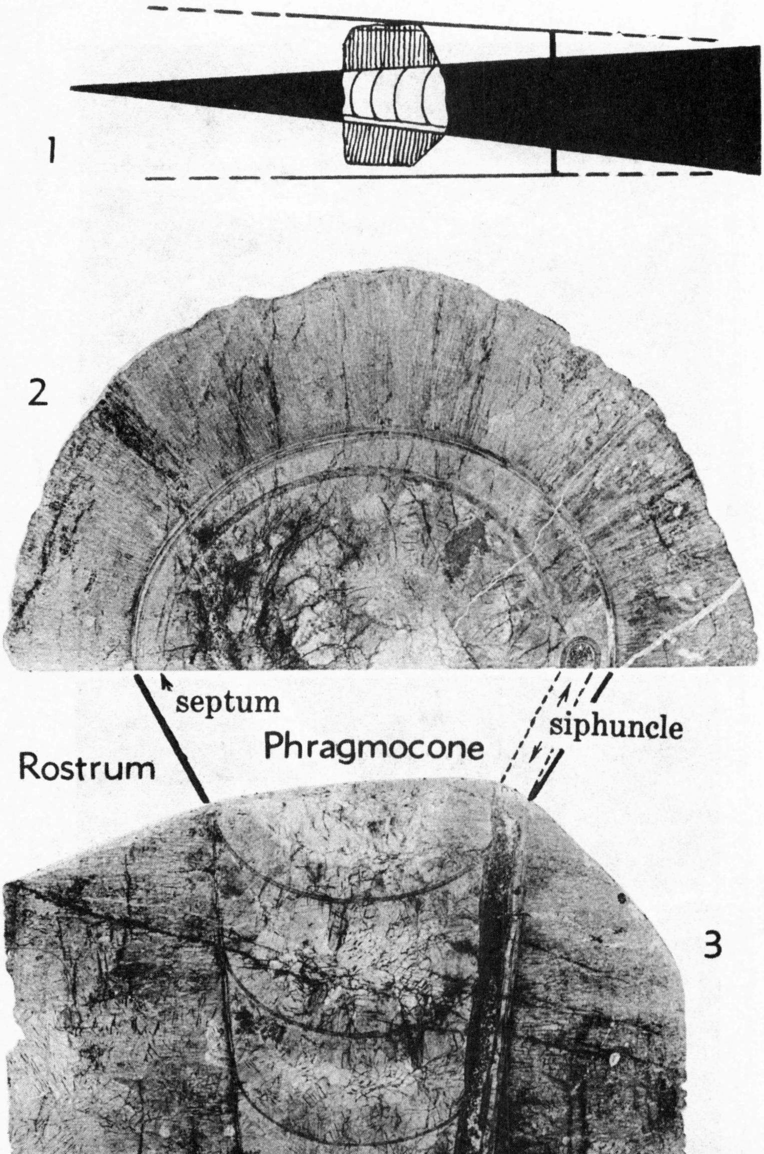
Plate 1. *Choanoteuthis mulleri,* holotype.

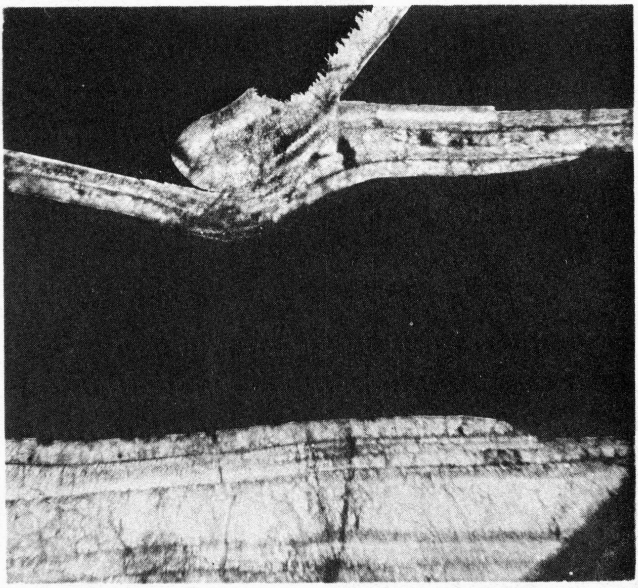
Fig. 1. Longitudinal thin-section, shown in relation to the restored alveolar position of the rostrum. (Drawing)

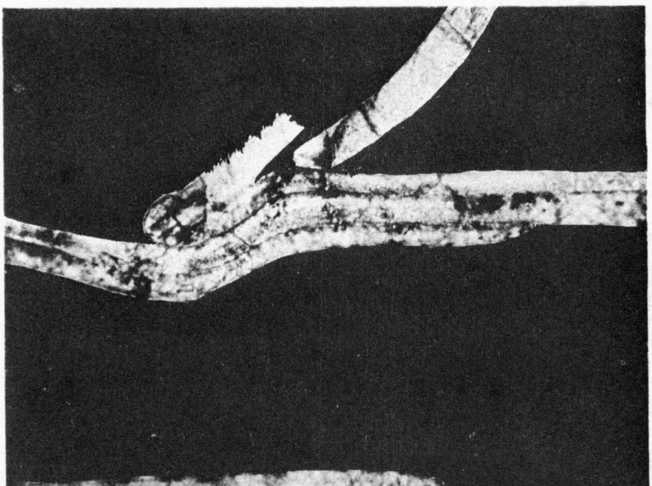
Fig. 2. Transverse thin-section, x 4. A septum is intersected near its junction with the shell wall. The siphuncle is not quite marginal. (Unretouched photograph.)

Fig. 3. Longitudinal thin-section, x 4. In this section the siphuncle is marginal. (Unretouched photograph.)


1
2
septum
siphuncle
Phragmocone
Rostrum
3

1





2

chambers. *Megateuthis*, in contrast to *Choanoteuthis*, has an excentrically located phragmocone, a large angle of expansion, and short chambers.

Choanoteuthis represents the first record of elaborate, *i.e.* nonorthochoanitic, siphuncular structure among pre-Jurassic belemnoids. Paradoxically, its siphuncle is also the most elaborate one known among belemnoids, regardless of age. The phylogenetic history of belemnoid siphuncles thus appears to parallel to some degree that of the nautiloids, both groups having developed holochoanitic forms at the time of their first great morphologic radiation and their rise to abundance, which in the case of the nautiloids lies in early Ordovician and in the case of belemnoids in Triassic time.

Genotype.—The genotype of *Choanoteuthis* is *C. mulleri* n. sp., from the Norian of Nevada.

Choanoteuthis mulleri n. sp.

Plate 1, figs. 1-3, Plate 2, figs. 1-2, Text fig. 1

The holotype and only specimen is represented by two thin-sections of the mid-alveolar region, one a dorso-ventral longitudinal section, the other transverse.

Rostrum.—The portion of the rostrum at hand (plate 1) shows a roughly circular cross-section with a diameter of 19 mm. in the transverse section (plate 1, fig. 2). The ventrolateral quadrants are slightly flattened. The surface is smooth, devoid of sulci, costae, or vascular furrows. The rostrum appears to thicken slightly apicad. As the adapical and adoral portions of the rostrum are missing, the length, overall shape, and the presence or absence of furrows in these areas remain undetermined. The interior of the rostrum is composed of calcite prisms, considerably coarser than the fibers found in well-preserved Jurassic and Cretaceous belemnite rostra. It is not certain whether these prisms represent the original structure, or whether they have been secondarily (diageneti-

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Plate 2. Siphuncle of *Choanoteuthis mulleri,* holotype, x 62.

Fig. 1. Foramen of the third septum (s3) in longitudinal thin-section. Funnels of septa 5 (f5) and 4 (f4) lap over neck of septum 3; f5 wedges out a little way behind septum 3, leaving f4 and f3 to continue apicad.

Fig. 2. Foramen of the second septum (s2) in longitudinal thin-section. Funnels of septa 3 (f3) and 4 (f4) lap over septum 2; a short way behind septum 2, f4 wedges out, leaving only f3 and f2 to continue apicad.

cally) produced by the reorientation and integration of adjacent fibers. The writer is inclined to favor the second alternative, particularly as the absence of growth lines (*laminae obscurae*) in all but the innermost portions of the rostrum suggests alteration.

Conch.—The longitudinal section of the conch includes three complete chambers in the mid-alveolar region (text fig. 1, plate 1, figs. 1, 3). The angle of divergence is 11.5°. In cross-section (plate 1, fig. 2) the conch appears to be slightly oval, measuring 12.2 mm. dorso-ventrally at a lateral diameter of 11.8 mm. The chambers show the following length-height dimensions (the height of each chamber being measured dorso-ventrally at the suture of the adapically bounding septum) 2.5 : 6.2 mm.; 2.8 : 6.7 mm.; 3.3 : 7.3 mm.; 3.8 or more : 7.9 mm.

The conotheca and septa, presumably originally of aragonite, have become recrystallized to calcite, but despite the attendant loss of microstructure the individual shell layers have largely remained distinct. The conotheca shows two well-defined layers (text fig. 1). The thin *annulus-layer* of Nautilus is either wanting or not recognizable. The septa show no layering. Their areas of adnation are rather broad, as the septa wedge out gradually in orad direction, and are supported on the adapical side by deposits similar to those found in *Nautilus*. The septa are not prolonged along the dorsal wall, but along the venter they extend farther orad than on the dorsum, forming what may be a short mural tongue or a ventral saddle (alternatives which cannot be decided from the thin-sections at hand).

Siphuncle.—The siphuncle lies at or near the ventral margin; in the longitudinal section the material between the conotheca and the lumen of the siphuncle appears to be almost entirely taken up with thick septal matter (mural parts and septal necks), whereas the transverse section (plate 1, fig. 2) shows the siphuncle separated from the conotheca by 0.1 mm. of chamber-filling matrix. In this section the siphuncle is distinctly broader than high. As seen in text figure 1 and plate 2, the siphuncle is constricted at the septal foramina, and expanded in the chambers. Its wall is approximately 0.1 mm. thick, *i.e.* comparable in thickness to septa or conotheca, is calcareous, and consists of two or, just behind each septum,

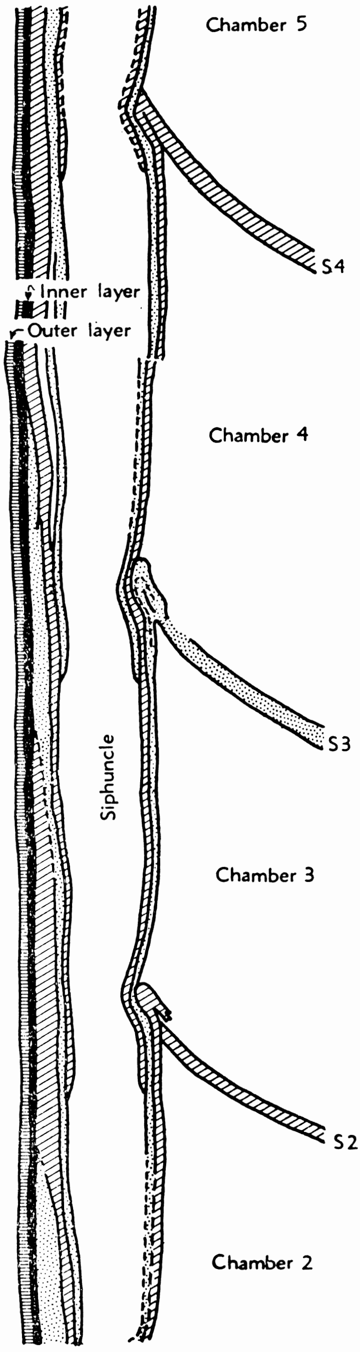

Fig. 1. ***Choanoteuthis mulleri***, holotype, x 25. Diagram of siphuncle, prepared from a photographic enlargement of the longitudinal thin-section. The outer and inner layers of the shell wall are succeeded in the interior by the crowded septal funnels on the ventral margin of the siphuncle. Septa and their funnels are alternately cross-hatched and stippled to facilitate tracing.

three layers, (plate 2). Each of these layers is the apicad extension of a septum, constructed in the following manner: Each septum extends apicad around the septal foramen, into an extraordinarily long funnel (either a septal neck or a septal neck combined with a modified connecting ring) which lines the siphuncle through the first and second, into the third preceding chamber. Successive funnels are invaginated, thus producing the multiple wall of the siphuncle (text fig. 1).

Locality and repository.—The specimen was found by Dr. Siemon Muller at Loc. 781, in the Norian Gabbs formation of the Gabbs Valley Range, Nevada.

The specimens are deposited in the Stanford University Collections: the longitudinal section is no. 8027, the transverse section, no. 8028.

RELATIONSHIPS OF TRIASSIC BELEMNOIDS

Of various genera reported from the Triassic, eight appear to have some claim to validity. These are compared in table 1. Of them, only *Aulacoceras* Hauer and *Dictyoconites* Mojsisovics can be said to be reasonably well known; even among these such features as the shape of the proostracum and the details of shell structure remain to be discovered.

Naef (1922) and Flower (1944, 1947) have discussed the classification of these forms. Suffice it here to say that whereas most of the Triassic forms appear to have more strongly developed phragmocones than do the majority of Jurassic and Cretaceous belemnoids, various members of the "*Atractites* group" in other respects closely approach the morphology of the Jurassic belemnites. Indeed, it appears possible that *Atractites* includes, among others, stocks ancestral to the Jurassic Hastitinae, that *Metabelemnites* may be ancestral to the Belemnoteuthinae, and that *Choanoteuthis* may be a forerunner of the Passaloteuthinae. It is evident that the Triassic belemnoids represent a variety of stocks. In the past they have generally been lumped into a single family, the Aulacoceratidae Bernard. This family is probably not a natural unit, but it is felt that much morphologic information must be accumulated before a thoroughgoing reclassification is feasible.

The main problem to be solved before such a reclassification can be successful is the segregation of the various stocks which have been lumped in the genus *Atractites* Guembel. These

TABLE 1
Triassic belemnoid genera

		ROSTRUM			PHRAGMOCONE		SIPHUNCLE	RANGE
		Relative shape	Lateral furrows	Ornamentation	Alignment	Angle of expansion		
	Aulacoceras Hauer	fairly short, blunt	present	costate	straight, axial	5–12°	orthochoanitic	Upper Trias.
	Dictyoconites Mojsisovics	long, slender	”	costate	straight, axial	5–12°	”	Upper Perm.-Upper Trias.
	Actinoconites Stolley	long, slender	”	smooth	straight, axial	5–12°	?	Upper Trias.
"Atractites group"	*Atractites* Guembel	long, slender	absent	”	straight, axial	5–20°	orthochoanitic	Lower Trias.-Lias.
"Atractites group"	*Metabelemnites* Flower	short, blunt	”	”	straight, axial	12° ±	?	Upper Trias.
"Atractites group"	*Choanoteuthis* nov. gen.	?	”	”	straight, axial	11° ±	holochoanitic	Upper Trias.
	Calliconites Gemmelaro		present	”	slightly excentric	large	?	Upper Trias.
	Zugmontites Reis		?	”	curved, excentric		?	Middle Trias.

stocks resemble each other in possessing large, well calcified, straight phragmocones, and smooth rostra devoid of lateral furrows. Flower (1944) recognized the need for separating the various components. He attempted a division based upon the length of the post-alveolar portion of the rostrum, and recognized two groups: most of the species referred to *Atractites,* and typified by *A. ausseanus* Mojsisovics, possess a rostrum which extends far apicad beyond the tip of the phragmocone; *A. philippii* Hyatt and Smith, on the other hand, is characterized by a rostrum best developed in the alveolar region, terminating a short way behind the latter. Flower was not able to determine to which of these groups the type species, *Atractites alpinus* Guembel, belongs. He has therefore proposed that the genus *Atractites* be dropped, and that the majority of its members, characterized by apically extended rostra, be placed in the new genus *Ausseites* Flower (based on *Atractites ausseanus* Mojsisovics); furthermore, he has made *A. philippii* Hyatt and Smith the type species of the new genus *Metabelemnites* Flower, characterized by a rostrum extending only a little beyond the alveole.

There can be no question about the propriety of separating *Atractites philippii* from the forms possessing extended rostra. it is, however, to be regretted that Flower did not supplement Hyatt and Smith's figures (1905) with further illustrations and measurements of *Metabelemnites* in order to clearly illustrate the nature of the rostrum. It is also regrettable that neither illustrations nor measurements have been published for the rostrum of *Ausseites ausseanus,* the type species of the genus with which *Metabelemnites* is contrasted.

The writer feels that the advisability of dismissing the genus *Atractites* has not been adequately demonstrated. It appears highly probable that *Atractites* Guembel and *Ausseites* Flower are synonyms; until further facts have been brought to light, and an effort has been made to check the type specimens, the author will tentatively consider them as such.

Flower's subdivision of the Atractites group represents a step in the right direction; however, studies will have to be extended beyond surficial features. The discovery of the above-described *Choanoteuthis* points to diversity of siphonal structures among these forms, and Christensen's discoveries of cameral deposits in Jurassic belemnoids point to another feature of potential usefulness in classification. Much light has been shed on the relationships of Jurassic and Cretaceous belemnites by studies of the ontogeny of the rostrum, as seen in section; this method also remains to be applied to the *Atractites*-like forms of the Trias and Lias.

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