ISSN 0031-0301

PALEONTOLOGICAL JOURNAL

A TRANSLATION OF

ПАЛЕОНТОЛОГИЧЕСКИЙ ЖУРНАЛ

SCRIPTA TECHNICA, INC.
A Subsidiary of John Wiley & Sons, Inc.

VOLUME 26 NUMBER 2 1992
ENGLISH EDITION PUBLISHED AUGUST 1993

UDC 581.1:551.762.3/763.12(477.75) Paleontological Journal, 26(2), 1992

THE ONTOGENESIS OF SOME EARLY CRETACEOUS BELEMNOIDS

I. S. Barskov and A. F. Weiss

Moscow University; Paleontological Institute, Russian Academy of Sciences

Abstract: A method of studying belemnitid ontogeny on the basis of changes in proportions of the cross section of the rostrum is proposed. This article presents the results of a study of the ontogenesis of the rostra of 20 species (including *Duvalia nasuta* sp. nov. and *D. satelles* sp. nov.) of four genera: *Duvalia* Bayle et Zeiller, 1878, *Conobelus* Stolley, 1919, *Pseudoduvalia* Naef, 1922 (Duvaliidae Pavlow, 1913) and *Dicoelites* Boehm, 1906 (Dicoelitidae Sachs et Nalnjaeva, 1967). It is shown that the ontogenetic method can be used in systematics and in reconstructing phylogeneses.

* * *

It has long been known that the course of individual development of belemnoids and its stages are reflected in the rostrum. Quenstedt found a small rostrum, which he called an "embryo," in longitudinally broken Jurassic belemnites [6, 22]. Abel [13] and Stolley [25] have also written about the "embryonic rostrum" (since the rostrum is an ontogenetically later structure) and replaced it with "first visible rostrum," which is neutral with respect to the interpretation of the type of ontogeny [5, 6, 9, 11, 18, 19]. This term is usually understood to refer to the stage of development in which no growth lines can be seen within the rostrum. The concept of the "first visible rostrum" or "rostrum in the initial stage" even entered into the diagnoses of genera and species [3, 9, 10, 11]. But this particular structure originates in the diageneticprocess, and its identification is largely subjective. Another artefact is Hanai's [17, 24] ontogenetically earliest rostral formation—the "primordial rostrum" [2].

The stages of individual development in the belemnoids were more clearly formulated by Fischer [16], who distinguished three stages in the Permian *Dictyoconites groenlandicus* Fischer (Aulacoceratida): a nepionic, a neanic and an ephebic-gerontic (or juvenile, adult and senescent) stage.

The character of the changes at the boundaries of the various ontogenetic stages was considered in detail by Pugaczewska [20, 21], who found them in several Jurassic genera. She demonstrated the changes in proportions of the rostrum in the various stages, particularly in the

---

Translated from: Ob ontogeneze nekotorykh rannemelovykh belemnoidey. Paleont. zhur., No. 2, pp. 58-70, 1992.

ISSN0031-0301/92/0002-0070

proportions of its transverse section, and the differences at the boundaries of the growth stages, although these boundaries themselves were established visually and quite arbitrarily.

The aim of our research is to show the changes in shape of the rostrum within the growth stages, the direction and rate of change throughout each of them, and where their objective boundaries are in certain families Duvaliidae Pavlow, 1913 and Dicoelitidae Sachs et Nalnjaeva, 1967. Not only can different species be distinguished by the character of these changes, but also the closeness and relatedness of species, the possible phylogenetic links between them, and the evolution of their ontogenesis can be judged.

The family Duvaliidae is isolated in the systematics of the belemnoids, because of the dorsal position of its alveolar groove. In establishing this family, Pavlow [8] evidently included in it only the type genus *Duvalia* Bayle et Zeiller, 1878. Stolley [25] then added to this family the genera *Pseudobelus* Blainville, 1827 and *Conobelus* Stolley, 1919. Later additions to the family have been the genera *Pseudoduvalia* Naef, 1922 [19] (=*Polygonalia* Ak. Alizade, 1965 — objective synonym [1]), *Berriasibelus* Delattre, 1952 [15], *Rhopaloteuthis* Lissajous, 1915 [4, 11, 12, 20, 21], *Castellanibelus* Combemorel, 1973 [14], *Produvalia* Riegraf, 1981 with two subgenera [23].

Riegraf removed the genus *Rhopaloteuthis* from the duvaliids and considered it to be a subgenus of *Hibolithes* Montfort, 1808, in accordance with his nomenclatural typification of the species *Belemnites sauvanaui* d'Orbigny [23].

In revising the genus *Pseudobelus* on the basis of a large amount of material, Nerodenko not only excluded it from the Duvaliidae, but also established an independent family for it, which he combined with two new families into a new suborder—the Pseudobelina [7]. But the phylogenetic relationships of the duvaliids to the new suborder remain unclear, and it seems to us that they cannot be resolved without the ontogenetic data. We regard the monotypic *Berriasibelus* as a synonym of the genus *Conobelus*, to which we assign it as a subgenus, and *Castellanibelus* as a synonym of *Curtohibolites* Stoyanova-Vergilova, 1963, and exclude them from the duvaliids.

This article is based on a study of the Early Cretaceous *Duvalia*, whose membership in this family is not disputed. They include species of the genera *Dubalia*, *Conobelus*, *Produvalia* and *Pseudoduvalia*.

MATERIALS AND METHODS OF INVESTIGATION

We collected most of the specimens in 1986-1990. Additional materials were transmitted to us by our colleague, G. K. Kabanov, of the Paleontological Institute, Russian Academy of Sciences, to whom we are most grateful. In all, more than 100 specimens belonging to 20 species of four genera were studied (table 1).

We studied the transverse section through the rostrum at the boundary between the alveolar and the postalveolar parts, where the record of the growth line is fullest. The dorsoventral and lateral diameters were measured along all the visible growth lines on magnified photographs of the thin sections. Up to five measurements were thus made per 1 mm of the radius of the rostrum. Graphs were then drawn showing the relation of the degree of lateral compression (DV/LL) to the dorsoventral diameter (DV). If DV/LL = 1, the rostrum is perfectly

Table 1

Materials Studied

Species	No. sections		Locality	Strati-graphic interval	Spec. Nos.		
	trans-verse	longi-tudinal					
Conobelus (*Berri-asibelus*) *extinc-torius* (Raspail, 1829)	1	—	E. Crimea, Nanikovo	K_1v-h	4379/120		
C. (*Coctebelus*) *heres* Weiss, 1991	2	3	" Same, Yuzhnoye	 K_1v	4379/110 4379/203	4379/191 4379/204	4379/202
C. (*Coc.*) *kabanovi* Weiss, 1991	3	3	Same	 K_1v	2682/54 4379/199	2682/71 4379/200	4379/116 4379/201
C. (*Coc.*) *propin-quus* Weiss, 1991	2	1	Central Crimea, Mramornoye, Novoklenovo	K_1b	2681/194	4379/117	4379/207
C. (*Coc.*) *trique-trus* Weiss, 1991	1	—	E. Crimea, Nanikovo	K_1v-h	4379/105		
Conobelus (*Conobe-lus*) *barskovi* Weiss, 1991	1	—	Central Crimea, Novoklenovo	K_1b	4379/115		

C. (C.) conicus (Blainville, 1825)	1	—	" Same, Mramornoye	K_1b	4379/123			
C. (C.) incertus Weiss, 1991	1	—	E. Crimea, Yuzhnoye	K_1v	4379/119			
Dicoelites meyrati (Ooster, 1857)	3	—	" Same, Planer-skoye	J_2k-J_3o	4379/210	4379/211	4379/212	
D. sp.	5	—	" Same, Planer-skoye	J_2k-J_3o	4379/213 4379/216	4379/214 4379/217	4379/215	
Duvalia binervia (Raspail, 1829)	10	2	Central Crimea, Verkhorech'ye	K_1br-a	2578/3643 2578/3493 2578/1368	2578/3892 4379/80 4379/83	4379/82 4379/81 4379/85	4379/79 4379/82 4379/87
D. dilatata Blainville, 1825)	14	6	Central, E + SW Crimea; Bulgaria	K_1b-h	2578/126 2578/1306 2578/3903 2578/1047 2578/1661	2578/427 2578/409 43789/60 4379/64 4379/70	4379/59 4379/63 4379/62 4379/65 4379/71	4379/58 2681/54 4379/95 4379/67
D. emerice (Raspail, 1829)	2	—	Central Crimea, Mramornoye; Kuybyshev district	K_1h	2578/1627	2682/267		
D. grasiana (Duval-Jouve, 1841)	8	2	Novoklenovo, Verkhorech'ye, Kurskoye, Nani-kovo settlements	K_1br-a	2578/1064 4379/7 4379/17	4379/1 4379/8	4379/4 4379/10	4379/5 4379/16

Table 1 (continued)

Species	No. sections		Locality	Strati-graphic interval	Spec. Nos.			
	trans-verse	longi-tudinal						
D. lata (Blainville, 1825)	16	2	Central, E + SW Crimea	K_1b-h	2578/1065 2578/1708 4379/33 4379/44 4379/52	2578/1496 4379/28 4379/36 4379/45 4379/53	4379/26 4379/29 4379/42 2682/3	4379/27 4379/32 4379/43 4379/47
D. nasuta Barskov et Weiss, sp. nov.	3	—	Central Crimea, Novoklenovo	K_1br-a	2578/88	4379/89	4379/90	
D. satelles Barskov et Weiss, sp. nov.	3	—	" Same, Verkhorech'ye	K_1br-a	2578/3523	2678/1223	4379/91	
Pseudoduvalia crimica (Karakasch, 1907)	2	—	" Same, Mramor-noye	K_1h	4379/209			
P. tithonica (Oppel, 1865)	1	—	" Same, Novokle-novo	K_1b	4379/78			
P. sp	3	—	Nanikovo, Verkhorech'ye; Bulgaria	K_1h	4379/73	4379/75	4379/76	

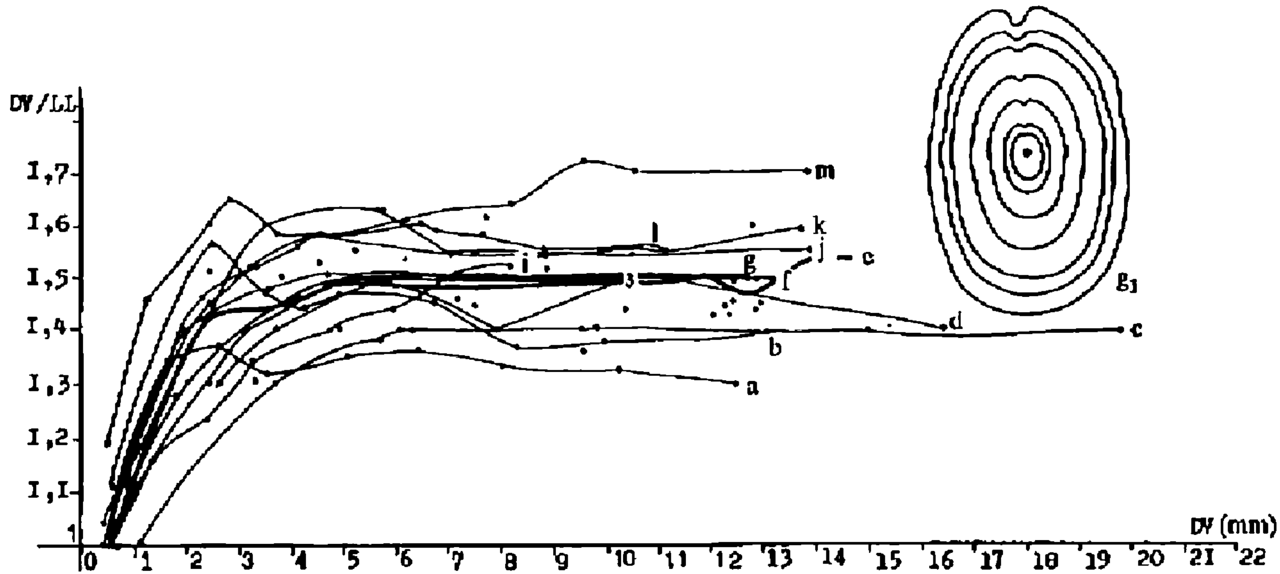

Fig. 1. Curves reflecting changes in degree of compression of rostrum and its transverse section at boundary between alveolar and postalveolar parts in *Duvalia lata*: *a* - Spec. 4379/32. I; *b* - Spec. 4379/32. II; *c* - Spec. 4379/27; *d* - Spec. 4379/44; *e* - approximated curve for species as a whole; *f* - Spec. 4379/43; *g*, *g*$_1$ - Spec. 2578/1496, *g*$_1$ - (×4.6); *h* - Spec. 2682/3; *i* - Spec. 4379/53; *j* - Spec. 2578/1065. I; *k* - Spec. 2578/1065. II. *l* - Spec. 2578/1708; *m* 4379/26.

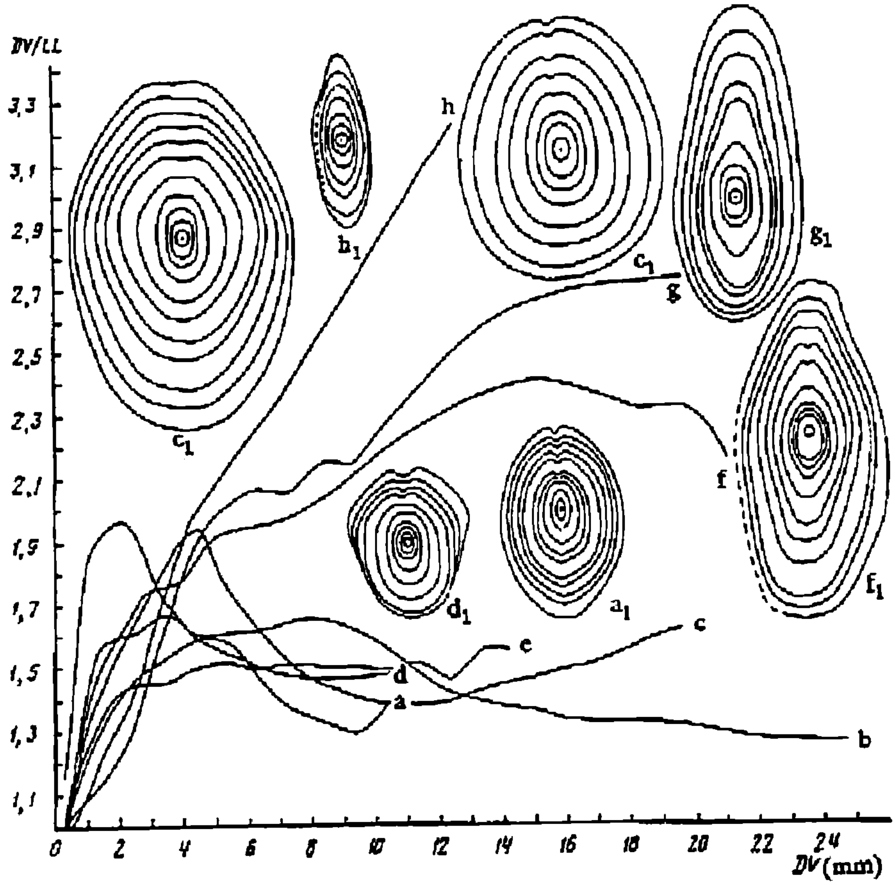

Fig. 2. Approximated curves of ontogenesis and transverse sections through rostra for seven species of *Duvalia*: *a*, a_1 - *D. nasuta*, a_1 - Holotype No. 2578/88 (×3.8); *b*, b_1 - *D. grasiana*, b_1 - Spec. 4379/7 (×2.8); *c*, c_1 - *D. satelles*, c_1 - Holotype No. 2578/3523 (×3.6); *d*, d_1 - *D. binervia*, d_1 - Spec. 2578/3892 (×3.3); *e* - *D. lata*; *f*, f_1 - *D. emerici*, f_1 - Spec. 2578/267 (×3.3); *g*, g_1 - *D. dilatata dilatata*, g_1 - Spec. 2578/186 (×3); *h*, h_1 - *D. dilatata binervoides*, h_1 - Spec. 4379/70 (×2.8).

round and there is no compression; if DV/LL > 1 the compression is lateral, and if DV/LL < 1 the compression is dorsoventral. The graph for *Dubalia lata* also shows the degrees of lateral compression of the juvenile rostra, whose dorsoventral and lateral diameters were measured at the level where the alveole begins.

DISTINCTIVE ONTOGENETIC FEATURES OF *Duvalia*

It was established that specimens of one species produce very similar curves of the relation of the degree of compression to the dorsoventral diameter, and that these individual curves can be approximated by one common curve for the whole species (fig. 1*e*).

Comparison of the curves for the seven species of *Duvalia* shows their distinct character in each species (fig. 2); these curves can serve as a diagnostic criterion in identifying the separate species.

Besides the purely numerical values of the proportions of the rostrum, the shape of its transverse section and the changes in it over the course of ontogenesis are also of important diagnostic significance. Thus, for example, very close numerical values of the changes in proportions of the transverse section and the form of the curves were obtained for the species *Duvalia binervia*, *D. nasuta* and *D. satelles*. But the shape of the transverse sections of their rostra differ (fig. 2*a*, *c*, *d*). In the adult stages of development of *D. binervia* the lateral sides are fairly flat, the section becomes pyriform, and the dorsolateral keels are clearly manifested. In *D. satelles* the section becomes oval and there is no flattening of the lateral sides. *D. nasuta* is characterized by an oval section with convex lateral sides, but in contrast to the two preceding species its section has a narrow and somewhat sharp, rather than fairly flat, dorsal side.

In the earliest growth stages of almost all the *Duvalia* species, when the dorsoventral diameter of the rostrum is up to 1 mm, there is a phase in which the rostrum is round (DV/LL—1). This phase is distinctly manifested in the old, Berriasian *D. lata* and *D. dilatata*, but reduced in the later forms, including the Hauterivian *D. lata*. In the Barremian-Aptian *D. nasuta* and *D. satelles* this stage is either reduced to 0.3-0.2 mm or else suppressed altogether.

In the next stage, which can be compared with the nepionic (in the terminology of Fischer and Pugaczewska), the changes in proportions of the rostral section in all the species studied are in the same direction: the degree of lateral compression increases rapidly (fig. 2, ascending parts of curves to DV = 2.4 mm). Moreover, the differences between species emerge clearly both in the degree of maximal compression attained by the rostrum in this stage and in the diameter at which this occurs (see below).

Species	DV/LL	DV, mm
Duvalia lata (Blainville, 1827)	1.6±0.05	3±0.5
D. dilatata (Blainville, 1827)	1.65±0.05	4±0.05
D. emerici (Raspail, 1829)	1.75±0.05	3±0.05
D. grasiana (Duval-Jouve, 1841)	1.75±0.05	3.5±0.05
D. binervia (Raspail, 1829)	1.73±0.04	3±0.05
D. nasuta sp. nov.	1.96±0.03	2.1±0.02
D. satelles sp. nov.	2±0.02	4.5±0.05

The next stage can be compared to the neanic stage of growth. The changes in the different species are in different directions (fig. 2): in *D. dilatata* and *D. emerici* as in *D. dilatata binervoides* Stoyanova-Vergilova, 1965, the degree of lateral compression continues to grow, but in *D. dilatata dilatata* and *D. emerici* at a slower rate (fig. 2*f-h*). In *D. lata* the degree of compression is stabilized at the highest level attained and thereafter remains practically unchanged (figs. 1, 2*e*). In the case of these species, one can speak of a three-stage ontogenesis. The ephebic-gerontic state, at least in *D. lata* and *D. dilatata binervoides*, cannot be discerned in the changes in shape of the rostral transverse section. Perhaps the stabilization of the compression that occurs at DV> 14-15 mm in *D. dilatata dilatata* and *D. emerici* indicates the beginning of the ephebic-gerontic stage.

A more complicated course of ontogenesis is characteristic of *D. grasiana, D. binervia, D. nasuta* and *D. satelles* (fig. 2*a-d*). The distinctly descending part of the curve testifies to a "reversal" of change in proportions of the transverse section. The degree of lateral compression decreases in *D. grasiana* to 1.2-1.3, in *D. binervia* to 1.25-1.45, in *D. nasuta* to 1.35-1.5 and in *D. satelles* to 1.28-1.38. In the first three of these species, the concluding stages of development are marked by a fairly sharp stabilization of the degree of compression, but in *D. satelles* the lateral compression again increases to DV/LL = 1.6. This probably characterizes the ephebic-gerontic stage in this species.

The simplest course of ontogenesis is characteristic of the oldest species *D. lata* and *D. dilatata*, which had already appeared in the Berriasian. In *D. lata* the nepionic stage, which is characterized by increasing lateral compression, is followed by its stabilization at the level attained. In the Berriasian *D. dilatata* lateral compression increases throughout the whole course of ontogenesis traced. In the Hauterivian species, the degree of compression is stabilized in the very last stages of development. The Hauterivian *D. emerici* inherits from its ancestor *D. dilatata* the simplest unidirectional course of ontogenesis, and not until the terminal stage does the lateral compression decrease somewhat.

A more complicated type of ontogenesis is characteristic of the Valanginian-Aptian *D. binervia*, as of the Barremian-Aptian *D. grasiana, D. nasuta* and *D. lata*. In these forms, after a particular degree of lateral compression has been attained, the direction of development reverses to the opposite direction and, in addition, additional stages of ontogenesis are manifested to various degrees.

If the degree of lateral compression of the rostrum has any adaptive value, a change in direction during ontogeny should indicate a change in adaptive ecologic niches during individual development. Thus it could be said that such species as *D. dilatata, D. emerici* and *D. lata* throughout both their juvenile and adult stages existed under the same conditions and led the way of life, whereas the adult *D. grasiana, D. binervia, D. nasuta* and *D. satelles* lived under conditions different from those of their juvenile growth stages. The decrease in lateral compression and formation of a more streamlined section through the rostrum perhaps indicates more active swimming and greater mobility in the adult stage of life.

The evolution of *Duvalia* shows a tendency toward the appearance of constantly increasing degrees of lateral compression in the nepionic stage: in the Berriasian *D. lata* amd *D. dilatata* it is 1.60-1.65, in the Hauterivian *D. emerici* 1.75, and in the Barremian-Aptian *D. nasuta* amd *D. satelles* it reaches 1.96-2.00. The duration of the first stage with a round rostrum also decreases to the point of complete disappearance. The duration of the nepionic stage also is

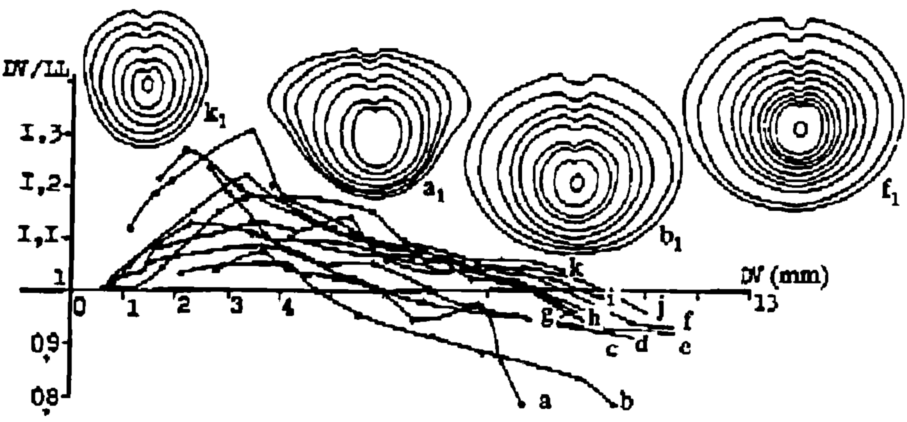

Fig. 3. Curves representing changes in degree of compression of rostrum and its transverse section at boundary of alveolar and postalveolar parts in eight species of *Conobelus*: *a*, a_1 - *C. Coctebellus) triquetrus*, Spec. 4379/105, a_1 - (×3.4); *b*, b_1 - *C. (Conobelus) incertus*, Spec. 4379/119, b_1 - (×3.4); *c*, *g*, *j* - *C. (Coc.) kabanovi*; *c* - spec. 2682/54, *g* - Spec. 4379/116, *j* - Spec. 2682/71; *d* - *C. (C.) barskovi*, Spec. 4379/115; *e* - *C. (C.) conicus*, Spec. 4379/123; *f*, f_1 - *C. (Berriasibelus) extinctorius*, Spec. 4379/120, f_1 - (×3.2); *h* - *C. (Coc.) heres*, Spec. 4379/110; *i*, *k*, k_1 - *C. (Coc.) propinquus*: *i* - Spec. 4379/117, *k*, k_1 - Spec. 2681/194, k_1 - (×4).

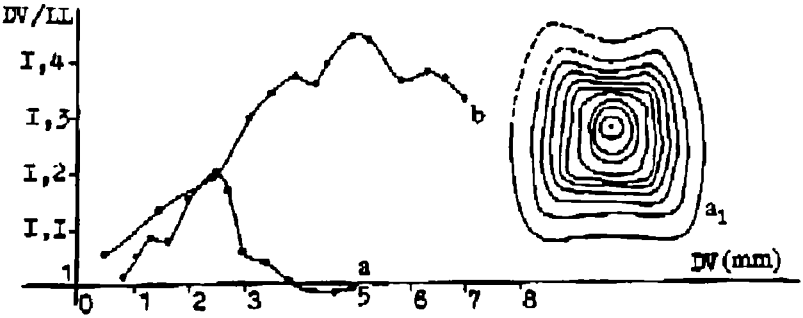

Fig. 4. Curves representing degree of compression of rostrum and its transverse section at boundary between alveolar and postalveolar stages in *Pseudoduvalia*: *a*, a_1 - *P.* sp., Spec. 4379/76, a_1 - (×5.8); *b* - *P. crimica*, Spec. 4379/209.

reduced. The maximal lateral compression is attained at increasingly smaller diameters—that is, individual development is accelerated.

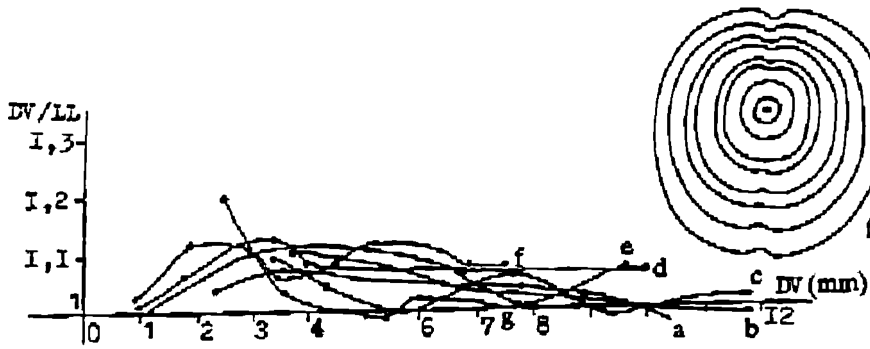

Fig. 5. Curves representing degrees of compression of rostrum and its transverse section at boundary between alveolar and postalveolar parts in *Dicoelites*: *a, c, d* - *D. meyrati*: *a* - Spec. 4379/218, *c* - Spec. 4379/219, *d* - Spec. 4379/220; *b, e-g* - *D.* sp.: *b* - Spec. 4379/215, *e* - Spec. 4379/214, *f*, f_1 - Spec. 4379/213, f_1 - (×5.7), *g* - Spec. 4379/216.

Comparison of the course of ontogenesis in the Conobelus, Pseudoduvalia *(Duvaliidae)* and *Dicoelites (Dicoelitidae)*. The curves of individual development in the eight species of *Conobelus* studied are distinctive for each species. In contrast to *Duvalia*, however, they do not show such strong differences between the separate species (fig. 3). In all the species of *Conobelus* the changes in proportions of the transverse section are closely similar, but its outline in the postnepionic stages of development differs sharply from one separate species to another: It may be oval, round, orsubtriangular with distinct costae. Thus it is likewise a characteristic diagnostic feature of the species, as in *Duvalia binervia*, *D. nasuta* and *D. satelles* considered above.

Close to those in *Conobelus* are the changes in proportions of the transverse section in *Pseudoduvalia* (fig. 4) and *Dicoelites* (fig. 5), although, as in *Conobelus* they are characterized by sharply different outlines in the later growth stages; subtetragonal in *Pseudoduvalia* (fig. 4a_1) and round in *Dicoelites* (fig. 5f_1).

Comparison of the courses of ontogenesis in the genera studied shows that all their representatives have the same direction of change in proportions of the transverse section through the rostrum in the nepionic stage—toward increasing degree of lateral compression. This attains its maximal level in the youngest *Duvalia* (DV/LL = 1.9-2.0); the minimal compression is characteristic of *Dicoelites* (DV/LL = 1.1-1.2), which can be regarded as the ancestral genus of the family Duvaliidae [11].

The postnepionic development differs substantially from one genus to another. As shown above, lateral compression in *Duvalia* is maintained in all subsequent stages of development, with particular features characteristic of each species. In *Dicoelites* the degree of lateral compression decreases in the neanic stage and thereafter remains at about one—that is, the transverse section becomes round. In *Pseudoduvalia* the degree of lateral compression also decreases, but the section takes on a subtetragonal outline. In *Conobelus* the lateral compression also decreases,

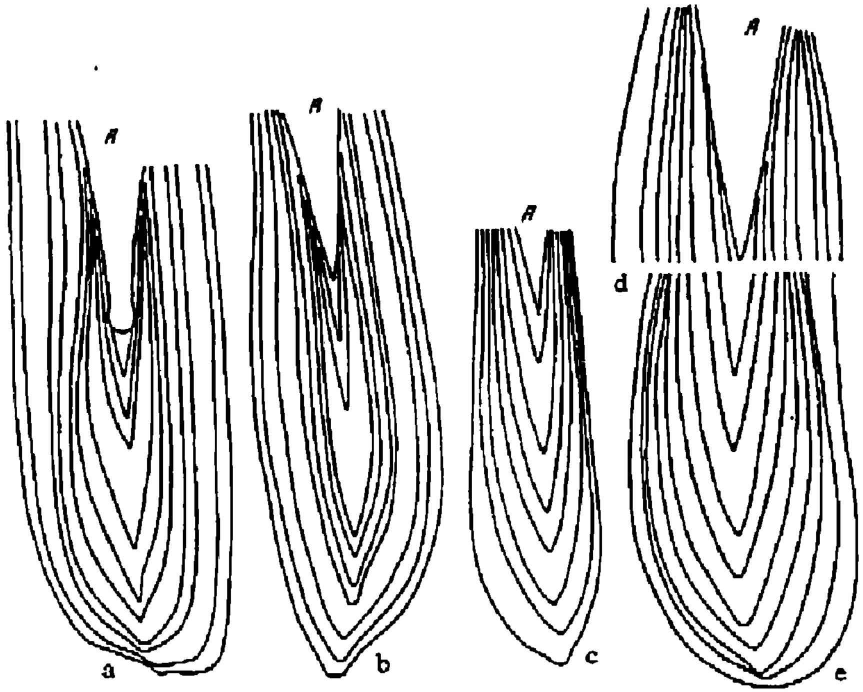

Fig. 6. Longitudinal sections through rostra of certain *Duvalia* (×2); *a* - *D. grasiana*, Spec. 4379/1; *b* - *D. lata*, Spec. 4379/29; *c* - *D. binervia*, Spec. 4379/81; *d*, *e* – *D. dilatata*: *d* - Spec. 4379/63, *e* - Spec. 2678/1306. *A* - alveole.

approaching one, and in a number of its species is replaced by dorsoventral compression (DV/LL <1).

The few data obtained by studying the changes in shape of the rostrum in the longitudinal dorsoventral sections permit only preliminary conclusions. According to the longitudinal outline of their rostrum in the early stages of development, *Duvalia* can be divided into two groups: those with asymmetrical and those with symmetrical rostra relative to the apical axis (fig. 6).

To the first group belong *Duvalia lata* and *D. grasiana*, in which even in the nepionic stage the dorsal side is straight and the ventral side convex, so that the tip of the rostrum is closer to the dorsal side (fig. 6*a*, *b*). *D. dilatata* and *D. binervia* in the nepionic stage have rostra of symmetrical outlines with the tip of the rostrum in the median position (fig. 6*c*, *d*). *D. binervia* quite rapidly takes on an asymmetrical outline with its tip closer to the dorsal side in the same degree as in *D. lata* and *D. grasiana*. In *D. dilatata* the asymmetry appears only in the latest growth stages, when the tip of the rostrum becomes round and what seems to be a second tip appears. This feature is characteristic largely of the later, Hauterivian representatives of this species.

Thus two lines of development can be discerned in the Early Cretaceous representatives of *Duvalia*. One of these lines consists of forms initially symmetrical in longitudinal section, originating from *D. dilatata*: *D. binervia*, *D. nasuta* and *D. satelles* — and only later taking on an asymmetrical outline, with the tip closer to the dorsal side. In the other line, that of *D. lata*—*D. grasiana*, the rostrum from the very earliest growth stages has an asymmetrical outline in longitudinal section.

MAIN CONCLUSIONS

1. The *Duvalia* species studied differ clearly in the character of the ontogenetic changes in the proportions of the transverse section through their rostrum at the boundary between the alveolar and postalveolar parts, and this can serve as a species specific criterion. In combination with other criteria, the curve reflecting the ontogenesis of the transverse section can help in the identification of species.

2. The species of *Duvalia* that appeared successively in the Early Cretaceous show a tendency toward complication of the course of ontogenesis; this reaches its greatest complexity in the latest, Barremian-Aptian *D. nasuta* and *D. satelles*, which can serve as one of the criteria in the identification of these new species.

3. In the families of Duvaliidae (*Duvalia*, *Conobelus* and *Pseudoduvalia*) and Dicoelitidae (genus *Dicoelites*), the early (nepionic) stage of ontogenesis is characterized by the same course of changes in proportions of the transverse section, in the direction of increasingly greater lateral compression. Lateral compression is maintained in *Duvalia*; in the other genera, lateral compression decreases, approaching one, and the outline of the transverse section through the rostrum becomes round (*Dicoelites*) or subtetragonal (*Pseudoduvalia*); in *Conobelus* lateral grades into dorsoventral compression.

4. The similarity of the early stages of ontogenesis in the Early Cretaceous duvaliids and the Jurassic dicoelitids supports the hypothesis that the former are descendants of the latter.

FAMILY DUVALIIDAE PAVLOW, 1913

Genus *Duvalia* Bayle et Zeiller, 1878

Duvalia nasuta Barskov et Weiss, sp. nov.

Specific name. Latin *nasutus* (nasal).

Holotype. PIN, No. 2578/88; Central Crimea, Belogorskiy district, Novoklenovo settlement; Lower Cretaceous, Barremian-Aptian.

Description (figs. $2a_1$, $7a$-d). Rostrum of medium size. Outline in dorsoventral plane subconical or cylindrical, and asymmetrical—with almost straight dorsal and convex ventral side, more rarely almost symmetrical; outline in lateral plane subcylindrical. Lateral compression moderate. Apical end pointed and slightly excentric, closer to dorsal side. Transverse section subrhombic. Lateral sides slightly convex, sometimes with indistinct longitudinal depressions.

Dorsal and ventral sides narrow and carinate, ventral side somewhat drawn out. Furrow narrow and fairly shallow, reaching 1/3 to 1/2 total length of rostrum. Apical line central or slightly closer to dorsal side. Depth of alveole less than 1/4 total length of rostrum.

Dimensions in mm and ratios:

Spec. No.	R	DV	LL	DV/LL	a
Holotype PIN					
2578/88	42.0	10.5	7.0	1.5	9.5
4379/89	36.5	10.7	7.5	1.43	—
4379/90	35.1	10.2	7.5	1.36	8.0

Comparison. Differs from *D. dilatata* and *D. emerici* in subconical-subcylindrical, more regular shape of rostrum, moderate lateral compression, and subrhombic transverse section with carinate ventral side; from *D. lata* and *D. grasiana* in subrhombic instead of elliptical transverse section, shorter and narrow dorsal furrow, and less deep alveole; and from *D. binervia* in absence of deep longitudinal depressions on lateral sides and of dorsolateral keels, and in narrow and relatively short furrow; in addition, differs from all species mentioned above in character of changes in shape and proportions of transverse section during ontogenesis.

Material. Four specimens from locality at Novoklenovo.

Duvalia satelles Barskov et Weiss, sp. nov.

Specific name. Latin *satelles* (attendant).

Holotype. PIN, No. 2578/3523; Central Crimea, Verkhorech'ye settlement; Lower Cretaceous, Barremian-Aptian.

Description (figs. $2c_1$, *7d-h*). Rostrum large or medium-sized. Outline is dorsoventral plane subconical or subcylindrical and almost symmetrical, in lateral plane subcylindrical. Lateral compression moderate. Apical end pointed, and often bears spinule, which is central or somewhat closer to dorsal side. Transverse section oval, with convex lateral sides. Furrow on adult rostra wide and fairly shallow, reaching about half total length of rostrum. Apical line central. Depth of alveole less than 1/3 total length of rostrum.

Dimensions in mm and ratios:

Spec. No.	R	DV	LL	DV/LL	a
Holotype PIN					
2578/3523	67.0	20.1	12.8	1.57	26.5
2578/1223	40.7	9.5	6.9	1.38	15.3
4379/91	43.0	8.3	8.3	1.19	13.5

Comparison. Differs from *D. dilatata* and *D. emerici* in subconical-subcylindrical, more regular shape of rostrum with almost central pointed tip, moderate lateral compression, quite long and

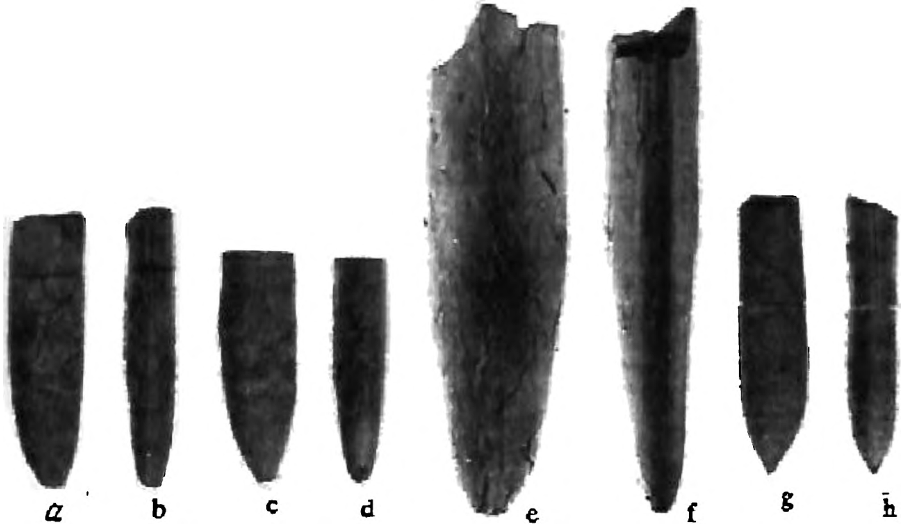

Fig. 7. New species of genus *Duvalia* (×1): *a-d* - *D. nasuta*; *a*, *b* - Holotype No. 4379[sic]/88; Central Crimea, Novoklenovo settlement; Barremian-Aptian; *c*, *d* - Spec. 4379/89, same locality and age; *a-c* - lateral side, *b-d* - dorsal side; *e-h* - *D. satelles*: *e-f* - Holotype No. 2578/3523; Central Crimea, Verkhorech'ye settlement; Barremian-Aptian; *g*, *h* - Spec. 2578/1223, same locality and age; *e*, *g* - lateral side, *f*, *h* - dorsal side.

distinct dorsal furrow and deeper alveole; from *D. lata* and *D. grasiana* is more symmetrical outline of rostrum with shorter and shallower groove; from *D. binervia* in absence of longitudinal depressions on lateral sides and of dorsolateral keels; and from *D. nasuta* in oval, not subrhombic transverse section and absence of dorsal and ventral keels; in addition, differs from last and above species in course of changes in shape and proportions of transverse section during ontogenesis.

Material. Three specimens from locality at Verkhorech'ye.

REFERENCES

1. Alizade, Ak. A., 1965, A new genus of the family Belemnitidae. Paleont. zhur., No. 3, pp. 142-144.
2. Barskov, I. S., 1973, On the structure of the protoconch and the ontogenesis of belemnites (Coleoidea, Cephalopoda). Doklady AN SSSR, Vol. 208, No. 2, pp. 439-442.
3. Gustomesov, V. A., 1964, Upper Jurassic Boreal belemnites (Cylindroteuthinae) of the Russian platform. Tr. Geol. in-ta AN SSSR, No. 107, pp. 91-211.
4. Gustomesov, V. A. and Ye. A. Uspenskaya, 1968, On the genus *Rhopaloteuthis* (Belemnitidae) and its Crimean representatives. Byul. MOIP, Otd. geol., Vol. 43, No. 5, pp. 65-78.
5. Krymgol'ts, G. Ya., 1939, Nizhnemelovyye belemnity Kavkaza (Lower Cretaceous Belemnites of the Caucasus). Monografii po paleont. SSSR (Monographs on the Paleontology of the USSR), GONTI Press, Moscow-Leningrad, Vol. 67, No. 1, 51 pp.

6. Naidin, D. P., 1969, Morfologiya i paleobiologiya verkhnemelovykh belemnitov (The Morphology and Paleobiology of the Upper Cretaceous Belemnites). Moscow Univ. Press, Moscow, 290 pp.
7. Nerodenko, V. M., 1986, On the systematic features of *Pseudobelina* (Belemnitida). Article filed at UkrNIINTI April 2, 1986, No. 943, Kiev, 32 pp.
8. Pavlow, A. P., 1913, Yurskiy i nizhnemelovyye Cephalopoda Severnoy Sibiri (Jurassic and Lower Cretaceous Cephalopoda of Northern Siberia). Zap. Imp. Ross. Akad. nauk, Ser. 8, Vol. 21, No. 4, 68 pp.
9. Saks, V. N. and T. I. Nal'nyayeva, 1964, Verkhneyurskiye i nizhnemelovyye belemnity Severa SSSR. Rody *Cylindroleuthis* and *Lagonibelus* (Upper Jurassic and Lower Cretaceous Belemnites from the North of the USSR. Genera *Cylindroleuthis* and *Lagonibelus*). Nauka, Leningrad, 166 pp.
10. Saks, V. N. and T. I. Nal'nyayeva, 1967, On the systematics of the Jurassic and Cretaceous belemnites. In: Probl. paleont. obosnovaniya detal'noy stratigr. mezozoya Sib. i Dal'n. Vostoka (Problems of the Paleontological Documentation of the Detailed Mesozoic Stratigraphy of Siberia and the Soviet Far East). Nauka, Leningrad, pp. 6-27.
11. Saks, V. N. and T. I. Nal'nyayeva, 1975, Ranne- i sredneyurskiy belemnity Severa SSSR. Megateuthinae i Pseudodicoelitinae (Early and Middle Belemnites from the North of the USSR. Megateuthinae and Pseudodicoelitinae). Nauka, Moscow, 190 pp.
12. Stoyanova-Vergilova, M., 1969, Representatives of the Jurassic genus *Rhopaloteuthis* in Bulgaria. Izv. Geol. int., Ser. paleont., Kn. 18, Sofia, pp. 97-104 [in Bulgarian].
13. Abel, O., 1916, Paläobiologie der Cephalopoden aus der Gruppe Dibranchiaten. Jena, 281 pp.
14. Combemorel, R., 1973, Les Duvaliidae Pavlow (Belemnitida) du Crétacé inférieur Français. Docum. Lab. Géol. Fac. Sci. Lyon, No. 57, pp. 131-185.
15. Delattre, M., 1952, Caractères et position systématique de *Berriasibelus extinctorius* (Rasp.) nov. gen. Bull. Museum Nat. Histoire Natur. Paris, Ser. 2, Vol. 24, No. 3, pp. 321-327.
16. Fischer, A. G., 1947, A belemnoid from the Late Permian of Greenland. Medd. Grönl., Vol. 135, No. 5, pp. 1-25.
17. Hanai, T., 1953, Lower Cretaceous belemnites from Miyako district, Japan. Trans. Japan. J. Geol. Geogr., Vol. 23, pp. 63-80.
18. Müller-Stoll, H., 1936, Beiträge zur Anatomie der Belemniten. Nova Acta Leopoldina., N. F., Vol. 4, No. 20, pp. 159-229.
19. Naef, A., 1922, Die fossilen Tintenfische. Eine paläozologische Monographie. Fischer, Jena, 322 pp.
20. Pugaczewska, H., 1957, O dwoch gatunkach belemnitow rodzaju *Rhopaloteuthis* z jury Polski. Acta Palaeontol. Polon., Vol. 2, No. 4, pp. 383-398.
21. Pugaczewska, H., 1961, Belemnoids from the Jurassic of Poland. Acta Palaeontol. Polon., Vol. 6, No. 2, 236 pp.
22. Quenstedt, F. A., 1849, Die Cephalopoden. Petrefactenkunde Deutschlands. Tübingen, Vol. 1, 580 pp.
23. Riegraf, W., 1981, Revision der Belemniten des Schwabischen Jura. Teil 8. Palaeontographica, Abt. A, Vol. 173, 1-4, pp. 64-139.
24. Spaeth, Ch., 1971, Untersuchungen an Belemniten des Formenkreises um *Neohibolites minimus* (Miller, 1826) aus dem Mittel- und Ober-Alb Nordwestdeutschland. Beih. Geol. Jahrb., Vol. 100, pp. 1-127.
25. Stolley, E., 1919, Die Systematik der Belemniten. Jahresber. Niedersachs. Geol. Ver. Hannover, Vol. 11, pp. 1-59.