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THE ONTOGENY AND SYSTEMATICS OF THE CALLOVIAN-OXFORDIAN BELEMNITES *Produvalia* AND *Pachyduvalia* FROM THE CRIMEA

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Abstract: The genus *Produvalia* is revised. According to the morphological and ontogenetic criteria, the subgenera *Produvalia* and *Pachyduvalia* can be regarded as having generic rank. The ontogenesis of the rostrum in *Produvalia* and *Pachyduvalia* was studied, and was found to be of the duvaliid type. The stages of ontogenesis are distinguished, the possibility of using ontogenetic criteria for the identification of species is demonstrated, and the new species *Pachyduvalia longa* is established. The phylogeny of the genera *Produvalia* and *Pachyduvalia* is derived on the basis of stratigraphic, morphological and ontogenetic data.

Проведена ревизия рода *Produvalia*. По морфологическим и онтогенетическим критериям подроды *Produvalia* и *Pachyduvalia* могут рассматриваться в рангах родов. Изучен онтогенез ростров *Produvalia* и *Pachyduvalia*, установлена его принадлежность к дювалиидному типу. Выделены стадии онтогенеза, продемонстрирована возможность использования онтогенетических критериев для идентификации видов и установлен новый вид *Pach. longa*. На основании стратиграфических, морфологических и онтогенетических данных сделаны выводы о филогении родов *Produvalia* и *Pachyduvalia*.

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The generic name *Produvalia* was first used by Schwegler [23] for Jurassic belemnites from Swabia with a short subcylindrical rostrum. Since Schwegler did not designate a type species, this name and its authority is a nomen nudum, and was erroneously included by Saks and Nal'nyayeva [8] as a valid name in the composition of the family Duvaliidae.

Translated from: Ontogeneticheskoye razvitiye i sistematicheskiy sostav belemnitovykh rodov *Produvalia* i *Pachyduvalia* iz kelloviya-oksforda Kryma.

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The genus *Produvalia* was validly distinguished, with two subgenera, only in 1981 by Riegraf [21]. The *Produvalia* from the Jurassic differ from the morphologically most similar Early Cretaceous species of the genus *Duvalia* in the less pronounced lateral compression of their rostrum in the adult stages. Riegraf suggested that the Early Cretaceous *Duvalia* and the Jurassic forms and different origins, which he was cited as an additional argument for the validity of the genus *Produvalia*. Reigraf considered that the composition of the nominative subgenus, with the type species *P.* (*P.*) *monsalvensis* (Gillieron, 1873), included the Jurassic (to the Tithonian inclusive) duvaliids previously assigned to *Duvalia*. In the original description the subgenus, besides its type species, included also *P.* (*P.*) *dumotieri* (Oppel, 1865) and *P.* (*P.*) *voironensis* (Favre, 1875). In addition, it can be considered to incorporate species described under the generic names *Duvalia*: *P.* (*P.*) *disputabilis* (Neumayr, 1871) [17, 20], *P.* (*P.*) *zaferai* (Combemorel, 1988), *P.* (*P.*) *rhopaliformis* (Combemorel, 1988), *P.* (*P.*) *rakotondrazafyi* (Combemorel, 1988) [11] and *Belemnites*: *P.* (*P.*) *duvaliana* (Orbigny, 1842-1849) and *P.* (*P.*) *didayana* (Orbigny, 1842-1849) [18].

In the composition of the subgenus *Pachyduvalia*, with type species *P.* (*P.*) *pinquus* Riegraf, 1981, were included species previously assigned to *Rhopaloteuthis* Lissajous, 1915, but having a dorsal alveolar furrow. This was an unambiguous nomenclatural resolution of the complicated taxonomic situation associated with the status of the genus *Rhopaloteuthis*.

In establishing *Rhopaloteuthis*, Lissajous [15] included in this composition the species having a dorsal furrow, yet as the type species he chose *Belemnites sauvanai* Orbigny, 1842 which, as shown in the illustration of its holotype [18, pl. 21, figs. 1-3, 6-8], has a ventral furrow. However, the taxa assigned to the Duvaliidae are characterized by a dorsal furrow, in contrast to other families, which have a ventral furrow. The development of a ventral furrow on the rostrum of the holotype of the type species of *Rhopaloteuthis*, contrary to the diagnosis of that genus, has led to various evaluations of the name *Rhopaloteuthis*. Some investigators [7, 22] have simply rejected it. Others [4, 9, 11, 12, 16, 19, 20] correctly acknowledging its nomenclatural appropriateness and on the basis of the diagnosis rather than the illustration of the type species, have considered the genus to belong to the family Duvaliidae; they explicitly or implicitly recognize the taxonomic exclusivity of the genus, which thus includes species with both a dorsal and a ventral furrow, depriving the whole family Duvaliidae of its diagnostic certainty. This view is clearly expressed by Gustomesov and Uspenskaya [4], who describe several new species of *Rhopaloteuthis* from the Jurassic of the Crimea with a definite dorsal furrow; one of them, in Gustomesov's opinion, also had a ventral furrow. Combemorel went even farther [12] by regarding as a synonym of *Rhopaloteuthis* the later established genus *Conobelus* Stolley, 1919, which has a furrow clearly in the dorsal position [25]. It is obvious that this completely disregarded the characterization of the type species of *Rhopaloteuthis*.

Therefore, it seems logical to accept Riegraf's proposal [21] to separate the forms with a dorsal furrow that were previously included in *Rhopaloteuthis* and place them in the taxon *Pachyduvalia* of subgeneric rank. The species in which the furrow is reliably known to be in the ventral position are assigned to *Rhopaloteuthis*, which is regarded as the subgenus of the genus *Hibolithes* Montfort, 1808 (family Belemnopsidae Naef, 1922). Besides the type species, it also includes the Kimmeridgian *Rhopaloteuthis somaliensis* Spath, 1935 from Somalia [24], which has a definite ventral furrow, and was chosen as the type species of the genus *Somalibelus* Jeletzky, 1972, family Belemnopsidae [14, 24]. It seems to us however, that justification is not sufficient for distinguishing a genus *Somalibelus*, which must thus be regarded as a younger synonym of the subgenus *Rhopaloteuthis*.

Of the almost twenty species that various authors have included in the genus *Rhopaloteuthis*, the dorsal position of the furrow has been reliably established in three: *Belemnites aenigmaticus* Orbigny, 1842-1849, *B. bzowiensis* Zeuschner, 1869, and *Rhopaloteuthis janischarensis* Gustomesov, 1968, which should be included in the composition of *Pachyduvalia*. At present, the species in *Rhopaloteuthis* in which the position of the furrow is not known but which morphologically form a homogeneous group with the three species above, can also be tentatively assigned to it. According to the combination of morphological features and the ontogenesis of the rostrum, this genus can incorporate 15 species with stratigraphic ranges from Bathonian to Kimmeridgian, inclusive.

No representatives of *Produvalia* have hitherto been mentioned from the Jurassic of the Crimea. Study of the Callovian-Oxfordian belemnites revealed two species of *P.* (*Produvalia*) and seven of *P. Pachyduvalia*. The latter include the forms previously described by Krymgol'ts [6] under the name *Hibolites* and by Gustomesov [4] under the name *Rhopaloteuthis*. Of these, *P. P. janischarensis*, as mentioned above, has a definite dorsal furrow.

There are no clear morphological criteria for identifying the above taxa if the phragmocone, or at least a fragment of it with the siphuncle, are not preserved. Additional diagnostic criteria, as shown by study of the ontogenesis of the genera *Duvalia*, *Conobelus* and *Pseudoduvalia*, may be the changes in form of the rostrum and particularly the proportions and outline of its transverse section during ontogenesis [1-3]. The closeness and relatedness of the species, the possible phylogenetic links between them, and the evolution of their ontogenesis cannot only be distinguished, but also judged by the character of these changes. As has been established and will be shown below, the substantial differences in ontogenesis of the rostrum between *P.* (*Pachyduvalia*) and *P.* (*Produvalia*) permit these taxa to be considered as having the rank of genera.

Materials and Methods of Study

In 1990 we collected about 100 specimens. We studied 36 specimens of nine species belonging to two genera, in both longitudinal and transverse section (table 1). For comparative material, we used data on the distinctive ontogeneses of the rostrum from other groups of duvaliids and dicoelitids [1-3], and also some belemnopsid (*Hibolithes*, *Belemnopsis*).

The most information came from the transverse section through the rostrum at the boundary between the alveolar and postalveolar parts, where the traces of the growth lines are the fullest. The dorsoventral and lateral diameters were measured in magnified polished sections on all clearly visible growth lines. Up to five such measurements were made per 1 mm of radius of the rostrum. Graphs were then drawn of the relationship of the degree of lateral compression (DV/LL) to the dorsoventral diameter (DV). If DV/LL = 1, the rostrum is circular, with no compression; if DV/LL > 1, the compression is lateral; if DV/LL < 1, the compression is dorsoventral. The specimens in any one species have very closely similar curves of the ratio of lateral compression to the dorsoventral diameter, or curves of ontogenesis. These ontogenetic curves can be approximated by one curve common to the species (fig. 1). These curves are particular to each species and can serve as one of the diagnostic criteria in identifying species. Among the other important diagnostic features are the transverse section and the changes in it (its measurements) during ontogenesis (fig. 2). It is the combination of these two characteristics that permits the species analyzed to be identified with maximal accuracy. In almost all the

Table 1

Table of Materials and Data

Species	No. of sections		Locality	Stratigraphic Interval	Spec. No.
	trans-verse	longi-tudinal			
Pachyduvalia agricolae	1	-	Eastern Crimea, Planer-skoye, Yanyshar Bay	J2 k3 - J3 j1	4379/292
P. bzowiensis	10	-	"	"	4379/260 4379/261 4379/262 4379/263 4379/273 4379/276 4379/280 4379/282 4379/297
P. gillieroni	2	2	"	"	4379/265 4379/266 4379/298 4379/299
P. kirae	2	-	"	"	4379/275 4379/267
P. longa	5	-	"	"	4379/286 4379/270 4379/272 4379/274
P. majeri	5	1	"	"	4379/268 4379/269 4379/289 4379/297
P. spissa	7	-	"	"	4379/271 4379/277 4379/279 4379/290 4379/291 4379/293 4379/285
Produvalia disputabilis	1	-	"	"	4379/254
P. voironensis	7	-	"	"	4379/250 4379/251 4379/252 4379/253 4379/255
Hibolithes	20	-	"	"	4379/300 4379/301 4379/302 4379/303 4379/304 4379/305 4379/306 4379/307 4379/308 4379/309 4379/310 4379/311 4379/312 4379/313 4379/314 4379/315 4379/316 4379/317 4379/318 4379/325

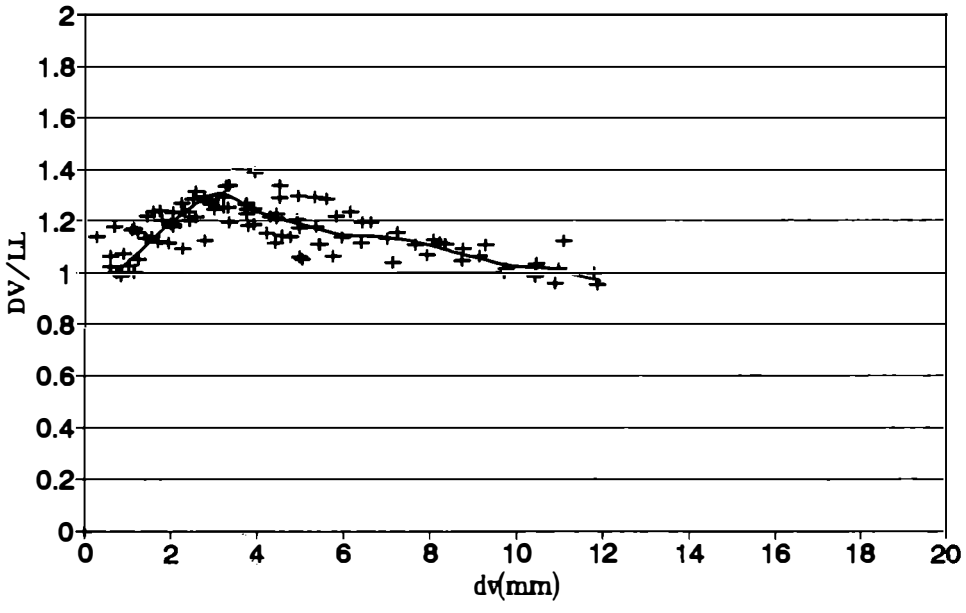

Fig. 1. Changes in degree of compression of rostrum during ontogenesis of 7 specimens and approximated ontogenetic curve for *Produvalia voironensis*. [No further explanation given, Ed.]

representatives studied of the families Duvaliidae (genera *Duvalia*, *Conobelus*, *Pseudoduvalia*) and Dicoelitidae (*Dicoelites*), in the earliest stages of development, at dorsoventral diameters of up to 1 mm, is a phase characterized by a circular rostrum (DV/LL ~ 1). In the next growth stage, the nepionic, in the terminology of Fischer [13] and Pugaczewska [20], the changes in proportions of the section through the rostrum in all species studied are in the same direction: the degree of lateral compression increases rapidly. In the next, the neanic, stage the changes are in different directions. The ephebic-gerontic stage, finally, is characterized by stabilized compression of the rostrum or by its secondary increase. The boundaries of the ontogenetic stages can be established by the points of alternation of the direction of change in the proportions of the rostrum. In the duvaliids and dicoelitids studied, the nepionic stage of ontogenesis is characterized by the same course of change in proportions of the transverse section: toward ever increasing lateral compres-sion. This can serve as a taxonomic criterion of familial rank, common to all the genera in a family. This type of ontogenesis is called the "duvaliid" [1, 3].

Distinctive Features of Ontogenesis of Late Jurassic Produvalids and Pachyduvalids

The curves representing the ratio of the degree of lateral compression to the dorsoventral diameter of the rostrum in the two *Produvalia* and seven *Pachyduvalia* species fall into two groups, one of which undoubtedly belongs to the duvaliid type of ontogenesis (that of *Produvalia*), while the other more closely resembles the hibolithoid type of individual development (for example, *Pachyduvalia bzowiensis* (figs. 2, 3), although a transition from one type to the other can be traced in the combination of species.

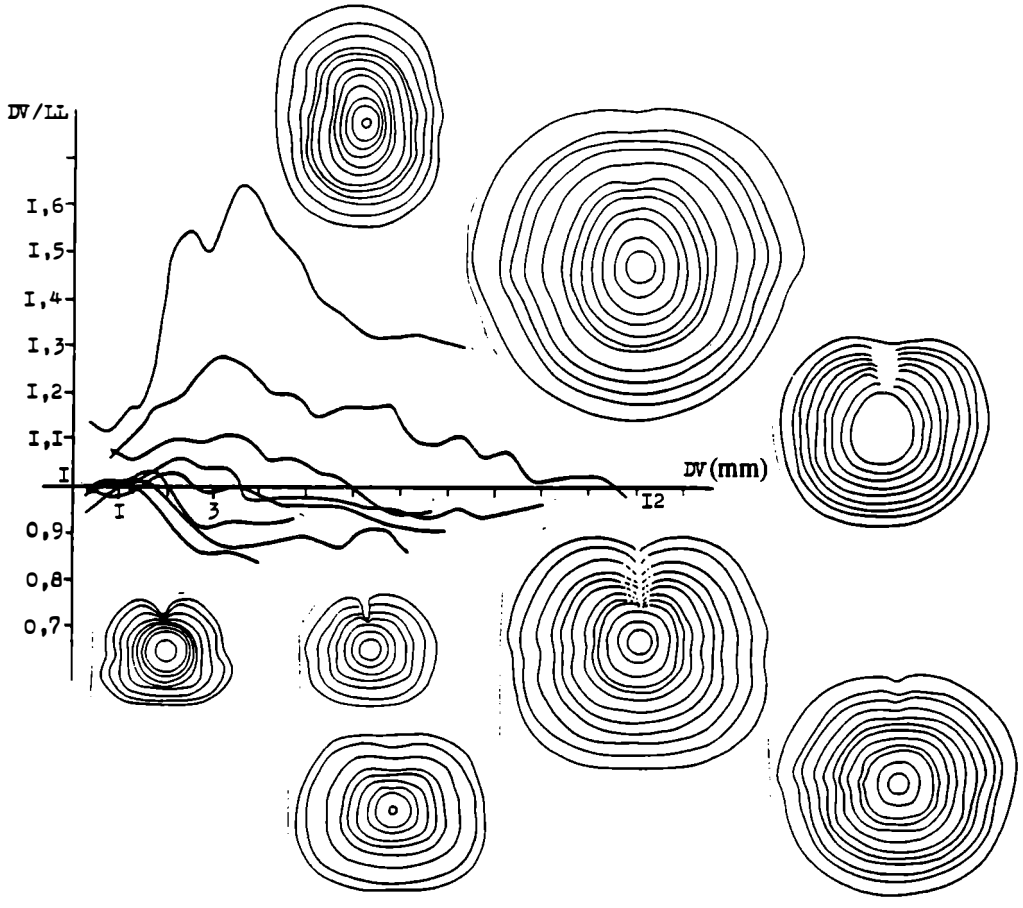

Fig. 2. Approximated ontogenetic curves and transverse section of 2 species of *Produvalia* and 6 species of *Pachyduvalia*: *a* - *Produvalia disputabilis*, *a*1 - Spec. No. 4379/254 (×2); *b* - *P. voironensis*, *b*1 - Spec. No. 4379/250 (×4.5); *c* - *Pachyduvalia spissa*, *c*1 - Spec. No. 4379/293 (×4.1); *d* - *P. majeri*, *d*1 - Spec. No. 4379/268 (×5); *e* - *P. gillieroni*, *e*1 - Spec. No. 4379/266 (×4); *f* - *P. kirae*, *f*1 - Spec. No. 4379/275 (×4); *g* - *P. longa*, *g*1 - Spec. No. 4379/272 (×5); *h* - *P. bzowiensis*, *h*1 - Spec. No. 4379/276 (×4.75); eastern Crimea, Planerskoye settlement, Yanyshar Bay; Upper Callovian-Lower Oxfordian.

In *Produvalia* the stage of a circular rostrum is not clearly manifested, but it is present at least in *P. voironensis*. In the nepionic stage the degree of lateral compression increases rapidly and reaches the following values:

Species	DV/LL	DV
Produvalia disputabilis	1.65	3.65 mm
P. voironensis	1.28 ± 0.1	3.4 ± 0.4 mm

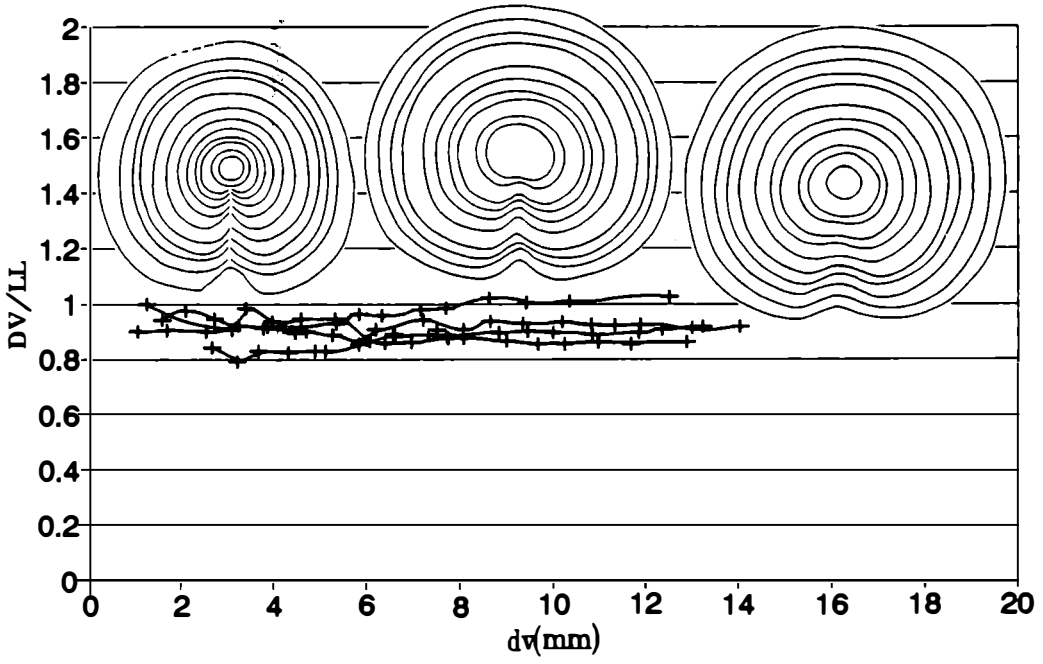

Fig. 3. Changes in degree of compression of rostrum during ontogenesis and transverse sections at boundary between alveolar and postalveolar parts and in postalveolar part of *Hibolithes hastatus* (Spec. No. 4379/310) (×3); *a*, a_1 - at base of alveole; *b*, b_1, *c*, c_1, *d* - in postalveolar part [letters *a* to *d* are not on figure, Ed.]; eastern Crimea, Planerskoye settlement, Yanyshar Bay; Upper Callovian-Lower Oxfordian.

In the neanic stage the degree of lateral compression decreases in both species, but more rapidly in *P. disputabilis*: at DV ~ 6.5 mm the lateral compression is DV/LL = 1.32, and thereafter is stabilized at this level in the concluding stage of development. In *P. voironensis* the lateral compression decreases more slowly and at DV ~ 11.5 mm eraches DV/LL = 1. At this stage the transverse section of *P. disputabilis* takes on a rounded-rectangular outline, and that of *P. voironensis* becomes rounded-trapezial, with a wider dorsal side and strongly developed lateral ridges.

Thus, ontogenesis in *Produvalia*, as in *Conobelus* and the older *Duvalia* species, is a three-stage process [1, 3]. The stabilization of the degree of compression as manifested in the last stage of individual growth in *P. disputabilis* can be regarded as the beginning of the gerontic process.

In *Pachyduvalia* the stage of a circular rostrum is manifested to various degrees: in *P. gillieroni* it is fully represented (up to DV ~ 1.3 mm), in *P. bzowiensis* and *P. majeri* it is reduced to DV ~ 0.3 mm, and in other species is perhaps missing altogether. The nepionic stage has different durations in the various species. In some it is strongly reduced. In this stage the rostrum is laterally compressed, and the different species differ both in degree of maximal compression and in the diameter of their rostrum at which it is attained:

Species	DV/LL	DV
Pachyduvalia spissa	1.11 ± 0.05	3.3 ± 0.1 mm
P. majeri	1.03 ± 0.02	2.3 ± 0.1 mm
P. gillieroni	1.06 ± 0.03	2.3 ± 0.1 mm
P. longa	1.03 ± 0.02	1.7 ± 0.15 mm
P. kirae	1.02 ± 0.01	1.45 ± 0.1 mm
P. bzowiensis	1.025 ± 0.02	0.9 ± 0.2 mm

In the neanic stage the changes in proportions of the transverse section through the rostra of all the species studied are in the same direction: the degree of lateral compression decreases, and the direction of compression changes to dorsoventral. This process occurs at different rates. The proportions at which DV/LL = 1 are reached in the various species at different DV values:

Species	DV
Pachyduvalia spissa	6.0 mm
P. majeri	2.6 mm
P. gillieroni	3.6 mm
P. longa	2.1 mm
P. kirae	1.75 mm
P. bzowiensis	1.3 mm

In this stage the transverse section through the rostrum in all species takes on an angular subtetragonal outline. Most species in the concluding stages of ontogenesis show a stabilization of the degree of dorsoventral compression of the rostrum that is more-or-less distinctly manifested, although this phenomenon was not established in *P. majeri*. The various degrees of compression and the dorsoventral diameter at which stabilization begins are shown below:

Species	DV/LL	DV
Pachyduvalia spissa	0.95 ± 0.03	6.8 mm
P. gillieroni	0.97 ± 0.02	3.7 mm
P. longa	0.91 ± 0.04	2.7 mm
P. kirae	0.87 ± 0.02	3.3 mm
P. bzowiensis	0.86 ± 0.04	2.8 mm

It is evident that here, as in the Early Cretaceous *Duvalia* [1], this stabilization characterizes the beginning of the ephebic-gerontic stage of ontogenesis.

At this point the question arises: how is the typically duvaliid type of ontogenesis in *Produvalia* related to the nearly hibolithoid type in *Pachyduvalia*? In other words, was the hibolithoid type of development in *Pachyduvalia* from hibolithoid ancestors, or did it arise from a primary duvaliid type, seemingly recapitulating the type of development of the forms ancestral to all the duvaliids? At present, the second alternative appears to be preferable, since, first, *Produvalia disputabilis* is one of the oldest duvaliids and was described from the Bajocian of Poland with certain dicoelitids [10, 17, 20], whereas the *Pachyduvalia* occur widely in the Callovian-Oxfordian. Second, all species of *Pachyduvalia* in the early stages of their development maintain the characteristically duvaliid direction of the change in proportions of the transverse section through their rostrum—the rise of lateral compression—even if the nepionic stage is considerably reduced.

The chronological succession of *Pachyduvalia* species shows a dominating tendency toward a decreasing degree of the lateral compression characterizing the rostrum in the nepionic stage (from 1.65 in *Produvalia disputabilis* to 1.01-1.015 in *Pachyduvalia bzowiensis*), and the duration of the nepionic stage is curtailed to DV < 1 mm. This also means a leveling out of the stage at which the rostrum is laterally compressed—that is, an acceleration of individual development. This type of evolution of ontogeny is characteristic of the duvaliids, as is the appearance of additional stages of ontogenesis, testifying to its complication. Hence, it can be concluded that the almost complete omission of the stage of lateral compression of the rostrum typical of certain *Pachyduvalia* species is a secondarily acquired characteristic.

The individual development of the rostrum was in the other direction (the hibolithoid type) in *Hibolithes* and *Belemnopsis* (family Belemnopsidae). Curves of the relation of the degree of compression rostral to the dorsoventral diameter in some genera are shown in figure 3. In the early stages of development, the nepionic stage (up to DV = 2-4 mm), the rostrum in these species is dorsoventrally compressed (DV/LL ~ 0.8). In the following stages of ontogeny the degree of dorsoventral compression is maintained or reduced, approaching the value of 1.0. If such a hibolithoid type of ontogenesis was original to *Produvalia*, in the nepionic stage the rostra of this genus should show the onset of dorsoventral compression.

We can thus conclude from the above that the ontogeny of *Pachyduvalia* is of the duvaliid type.

On the Phylogeny of *Produvalia* and *Pachyduvalia*

Study of the external and internal structure of the rostrum and, most important, its distinctive ontogenesis leads to certain conclusions concerning the phylogeny of the genera *Produvalia* and *Pachyduvalia*.

The first duvaliids, represented by the genus *Produvalia*, appeared in the Bajocian [20]. They already had the morphological features typical of most Late Jurassic—Early Cretaceous duvaliids. Thus, for example, the Bathonian-Oxfordian laterally compressed *Produvalia* were morphologically very close to the Early Cretaceous duvaliids: *Produvalia monsalvensis* and *P. didayana* from the Callovian-Oxfordian are very similar in the external features of their rostrum to the Early Cretaceous *Duvalia lata* and *D. grasiana*, *P. dumortieri* to *D. binervia*. Moreover, the curves of the relation of the degree of lateral compression to the dorsoventral diameter of the rostrum in a number of *Produvalia* species, on the one hand, and in *Duvalia* and *Conobelus* on the other hand, are almost the same.

In the Callovian, *Pachyduvalia* branched off from these generalized *Produvalia*. The rostrum in the initial species of *Pachyduvalia* shows moderate or slight lateral compression in the adult growth stages; in the chronological succession of *Pachyduvalia*, this grades into dorsoventral compression. The duration of the nepionic stage in which the rostrum is laterally compressed, as is characteristic of all the duvaliids, was reduced during the course of evolution of this genus, and the degree of compression in this stage decreased. The transverse section throughout the rostrum took on a tetragonal, pentagonal or trapezial outline, a number of species developed distinct ventrolateral keels (such as *Pachyduvalia bzowiensis*), and the rostrum became shorter and irregularly bulb-shaped. The dorsal furrow, which was very deep, and narrow, according to Gustomesov [4], may grade into an alveolar furrow. Some researchers [4, 5] have regarded this group as ancestral to the later duvaliids. However, the above tendencies in the evolution of their ontogeny and their morphological features rather indicate a high degree of specialization on the part of *Pachyduvalia*, in consequence of which this genus most likely had no descendants.

Thus, *Produvalia* can be considered the initial genus from which all the Late Jurassic and Early Cretaceous duvaliids were descended.

Pachyduvalia branched off from *Produvalia* at the Bathonian-Callovian boundary, and the first species of this new genus were characterized by a fully duvaliid type of ontogenesis (fig. 2). There is an almost complete coincidence between the curves of the relation of lateral compression of the rostrum to its dorsoventral diameter in *Pachyduvalia spissa* and those of certain *Conobelus* species. The chronological succession of *Pachyduvalia* species clearly shows a tendency toward decrease in lateral compression of the rostrum in the nepionic stage, as well as reduction of the duration of this stage. In view of this trend, the ontogenetic curves of the species of this genus can be arranged in the following evolutionary sequence: *spissa* → *gillieroni* → *majeri* → *longa* → *kirae* → *bzowiensis*, in which each species is the ancestor of the next one (fig. 2). But analysis of the outline of the transverse section and other morphological features of the rostrum, particularly its form and proportions, enables an important correction to be introduced into this series. Thus, in the outline of the rostral transverse section, the species of *Pachyduvalia* can be divided into two groups. The first group includes *P. majeri* and *P. kirae*, which have a subrectangular-subquadratic section, the second *P. gillieroni*, *P. longa* and *P. bzowiensis*, whose rostral section is rounded-trapezial or rounded-pentagonal (fig. 4). The validity of dividing these species into such groups is confirmed by analysis of the rostral morphology. The species of the first group have a shorter, more massive subcylindrical rostrum with a fairly blunt or round apex having a mucro, with a shorter postalveolar part, and a correspondingly deeper alveolus. The species of the second group have an elongated, irregularly clavate or subcylindrical rostrum with a pointed apex, also frequently having a mucro; their postalveolar part is elongated and the relative depth of the alveolus is accordingly quite small, so that the alveolus is often not preserved. *P. spissa*, the oldest species having morphological features typical of both groups, occupies an intermediate position and was obviously ancestral to the species of both groups.

Within the groups, based on the distinctive ontogeny of each particular species and its stratigraphic distribution (which, however, requires more thorough study), the initial forms can easily be distinguished. Thus, the original species of the first group is *P. majeri*, that of the second *P. gillieroni*.

Conclusions

1. The studied *Produvalia* and *Pachyduvalia* species clearly differ in the character of the onto-

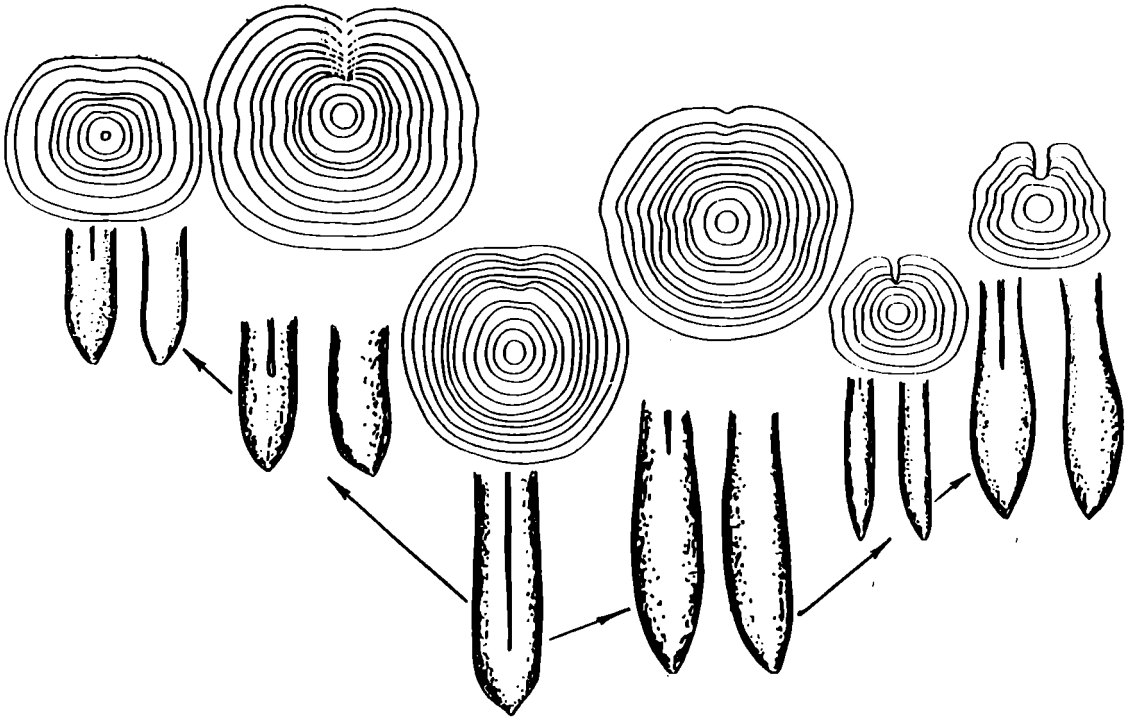

Fig. 4. Morphogenesis of Middle to Late Jurassic *Pachyduvalia.*

genetic changes in proportions of the transverse section through their rostrum at the boundary between the alveolar and postalveolar parts, and this difference can serve as a taxonomic criterion. This criterion, together with the distinctive form of the rostral transverse section, can be used to identify the species of these genera.

2. In *Produvalia*, the direction of change in proportions of the transverse section in all stages of ontogeny is the same in its general features as in other duvaliid groups. The evolution of *Pachyduvalia* shows a tendency toward complication and acceleration of ontogenesis, manifested in a reduction of the period of ontogenesis in which the rostrum is laterally compressed, and in a decrease in maximal values of this compression. This provides the basis for considering *Pachyduvalia* to have the rank of genus. Such a distinctive and obviously narrowly specialized group cannot have been ancestral to the Early Cretaceous duvaliids. This ancestral group may have been the earliest Middle Jurassic representatives of *Produvalia*, whose ontogenesis already shows the basic features of the duvaliid type.

The type specimens of the species below are in the Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow.

FAMILY DUVALIIDAE PAVLOW, 1913

Genus *Pachyduvalia* Riegraf, 1981

Rhopaloteuthis: Gustomesov, Uspenskaya, 1968, p. 66 (pars); Combemorel, 1988, p. 139 (pars).

Produvalia (*Pachyduvalia*): Riegraf, 1981, p. 106.

Type species. *Produvalia* (*Pachyduvalia*) *pinquus* Riegraf, 1981; Lower Oxfordian; western Germany.

Diagnosis. Rostrum medium-sized or small, clavate or subcylindrical. Compression dorsoventral, its degree varying widely. Apical end round with mucro or blunt and excentric, closer to dorsal side. Transverse section through rostrum subtetragonal (subquadratic or trapezial) or subpentagonal. Ventral side flat to various degrees. Ventrolateral ridges developed in a number of species. Lateral lines strongly developed and having various configurations. Numerous species with longitudinal lateral depressions in upper half of rostrum. Dorsal furrow short, less than 1/3 total length of rostrum, and very deep; alveolar furrow possibly present. Alveolus and apical line straight or slightly curved, central or excentric. Depth of alveolus reaching 1/3 total length of rostrum.

In nepionic stage of ontogenesis rostrum taking on slight degree of lateral compression (up to DV/LL < 1.1), in neanic stage becoming dorsoventral; latter sometimes considerable (up to DV/LL < 0.8). Transverse section in nepionic stage round or elliptical, in neanic stage subtetragonal or subpentagonal.

Specific composition. Sixteen species: *Pachyduvalia pinquus* (Riegraf, 1981), *P. aenigmatica* (Orbigny, 1842-49), *P. agricolae* (Parona et Bonarelli, 1895), *P. argoviana* (Mayer, 1863), *P. bzowiensis* (Zeuschner, 1869), *P. clavata* (Malecki, 1985), *P. gillieroni* (Mayer, 1866), *P. janischarensis* (Gustomesov, 1968), *P. kirae* (Gustomesov, 1968), *P. longa* sp. nov., *P. majeri* (Alth, 1875), *P. mulleri* (Gillieron, 1873), *P. quinquencialis* (Malecki, 1985), *P. spissa* (Gillieron, 1873), *P. urszuli* (Malecki, 1985). Seven species are known from Crimea (table 1, fig. 5).

Comparison. Differs from *Duvalia* and *Produvalia* in shorter, clavate or subcylindrical form and dorsoventral compression of rostrum, flatter ventral side, narrow and deep furrow, and tetragonal or pentagonal transverse section; from *Conobelus* in flatter ventral but not dorsal side of rostrum, narrow and deep furrow, tetragonal or pentagonal transverse section and distinct lateral lines; from *Pseudoduvalia* in clavate rostrum, deep furrow; and also from this and all other above genera in distinctive features of change in form and proportions of transverse section through rostrum during ontogenesis (fig. 2).

Pachyduvalia longa Barskov et Weiss, sp. nov.

Specific name. Latin *longus* (long).

Holotype. PIN No. 4379/274; eastern Crimea, Planerskoye settlement, Yanyshar Bay; Upper Callovian-Lower Oxfordian.

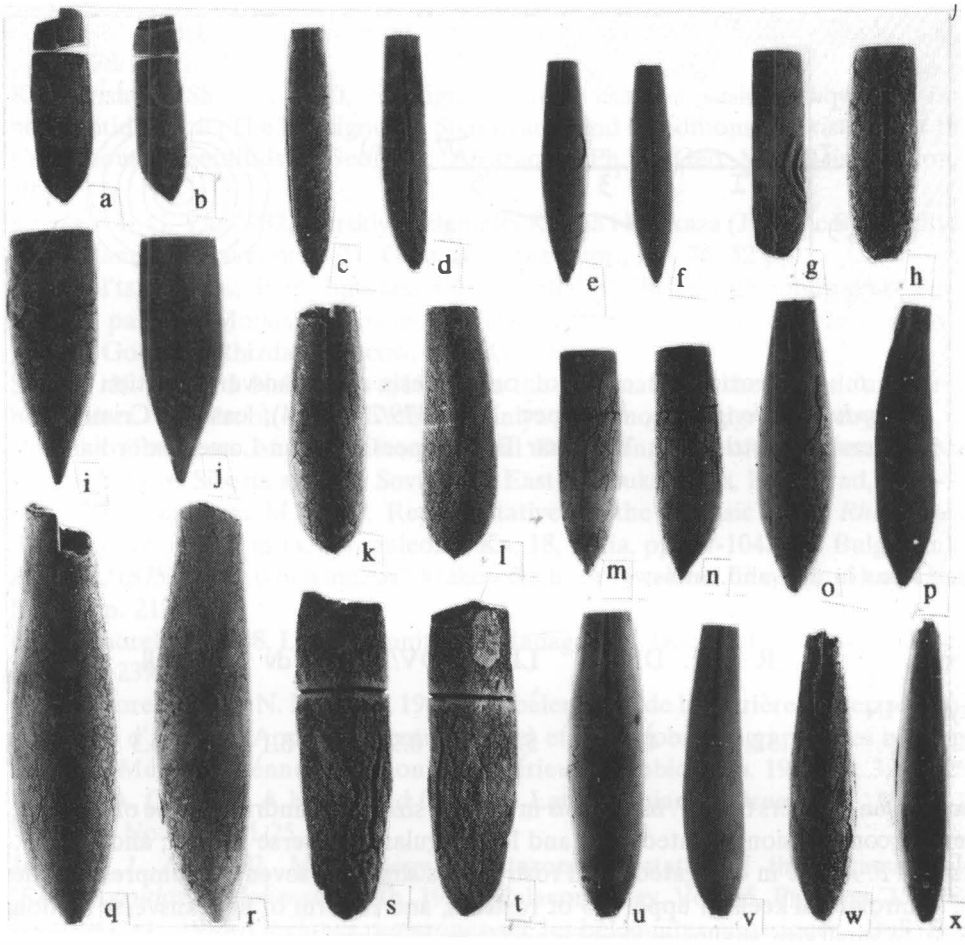

Fig. 5. Rostra of *Produvalia* and *Pachyduvalia* (×1); eastern Crimea, Planerskoye settlement, Yanyshar Bay; Upper Callovian-Lower Oxfordian; *a, b* - *Pachyduvalia kirae* (Gustomesov); Spec. No. 4379/275; *c-f* - *P. longa* sp. nov.: *c, d* - Holotype PIN No. 4379/274; *e, f* - Spec. No. 4379/270; *g, h* - *Poduvalia disputabilis* (Neumayr); Spec. No. 4379/254; *i, j* - *Pachyduvalia agricolae* (Parona et Bonarelli); Spec. No. 4379/292; *k, l* - *P. majeri* (Alth); Spec. No. 4379/268; *m, n* - *P. spissa* (Gillieron); Spec. No. 4379/271; *o, p, u-x* - *P. bzowiensis* (Zeuschner): *o, p* - Spec. No. 4379/260; *u, v* - Spec. No. 4379/258; *w, x* - Spec. No. 4379/259; *q, r* - *P. gillieroni* (Mayer); Spec. No. 4379/265; *s, t* - *Produvalia voironensis* (Favre); Spec. No. 4379/250; *a, c, e, g, i, k, m, o, q, s, u, w* - dorsal side; *b, d, f, h, j, l, n, p, r, t, v, x* - lateral side.

Description (fig. 5*c-f*). Rostrum is small, subcylindrical, subclavate, with point of maximal size at 1/3 to 1/4 total length of rostrum from apex. Dorsal side is almost straight, ventral is convex. Apical margin is fairly pointed; apex is central or slightly excentric, closer to dorsal side. Transverse section through rostrum at base of alveolus is rounded-trapezial. Ventral side is fairly flat. Carinate ventrolateral bends are visible in upper 1/3 of rostrum. Furrow is narrow; its length is 1/5 to 1/6 total length of rostrum. Lateral lines are clearly developed along whole length of rostrum as curved double lines. Alveolus and apical line are straight, central or slightly excentric. Depth of alveolus is no more than 1/6 total length of rostrum.

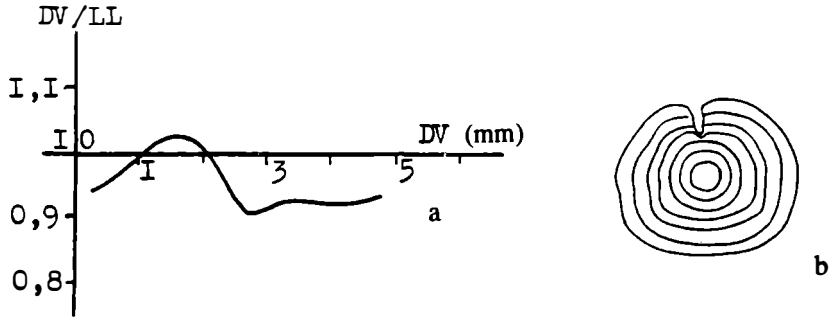

Fig. 6. Approximated curve of ontogenesis and transverse section of *Pachyduvalia longa* (*a*), *b* - Spec. No. 4379/272 (×4); eastern Crimea, Planerskoye settlement, Yanyshar Bay; Upper Callovian-Lower Oxfordian.

Dimensions in mm and ratios:

Spec.	R	DV	LL	DV/LL	dv	ll	dv/ll
Holotype PIN 4379/274	32	4.8	5.1	0.94	6.1	6.3	0.97

Comparison. Differs from *P. bzowiensis* in smaller size, subcylindrical shape of rostrum, lesser dorsoventral compression, pointed apex and less angular transverse section; and from *P. kirae*, *P. spissa* and *P. majeri* in elongated small rostrum, its slight dorsoventral compression, development of ventrolateral keels in upper 1/3 of rostrum, and in form of its transverse section; from *P. gillieroni* in small size, shallower alveolus and form of transverse section; and additionally from all above species in course of change in form of transverse section through rostrum during ontogenesis (fig. 6)

Distribution. Upper Callovian-Lower Oxfordian; Crimea.

Material. Six rostra from Yanyshar Bay.

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