

POLYMORPHISM IN THE JURASSIC AMMONOIDS¹

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Abstract: Polymorphism in Jurassic ammonoids is considered. Brady- and tachymorphic and brady- and tachygerontic shells and sexual dimorphs are distinguished. It is shown that particular types of sexual dimorphs characterize the various major taxa.

Key words: Cephalopoda; Ammonoidea; Jurassic; polymorphism.

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Variations in the shells of Jurassic ammonoids that can presumably be interpreted as manifestations of sexual dimorphism were mentioned long ago by such pioneering researchers as de Blainville [7] and d'Orbigny [13]. This matter became a subject of widespread discussion after special studies by Makowski [11] and Callomon [9]. At the present time, the occurrence of sexual dimorphism in the Jurassic ammonoids is generally accepted, and in descriptive monographs and articles, many morphs, species, or subgenera are boldly classed as males or females.

Other forms of stable intraspecific variation (tachy- and bradymorphy, tachy- and bradygeronticity), however, are more rarely discussed. During the past decade, primarily Russian publications have discussed these manifestations [3-6].

The purpose of this paper is to consider the types of polymorphism of Jurassic ammonoid shells and their possible interpretation. The data were obtained from a study of mostly Middle Jurassic and some Late Jurassic ammonitids of the Caucasus, Central Asia, and Central Russia.

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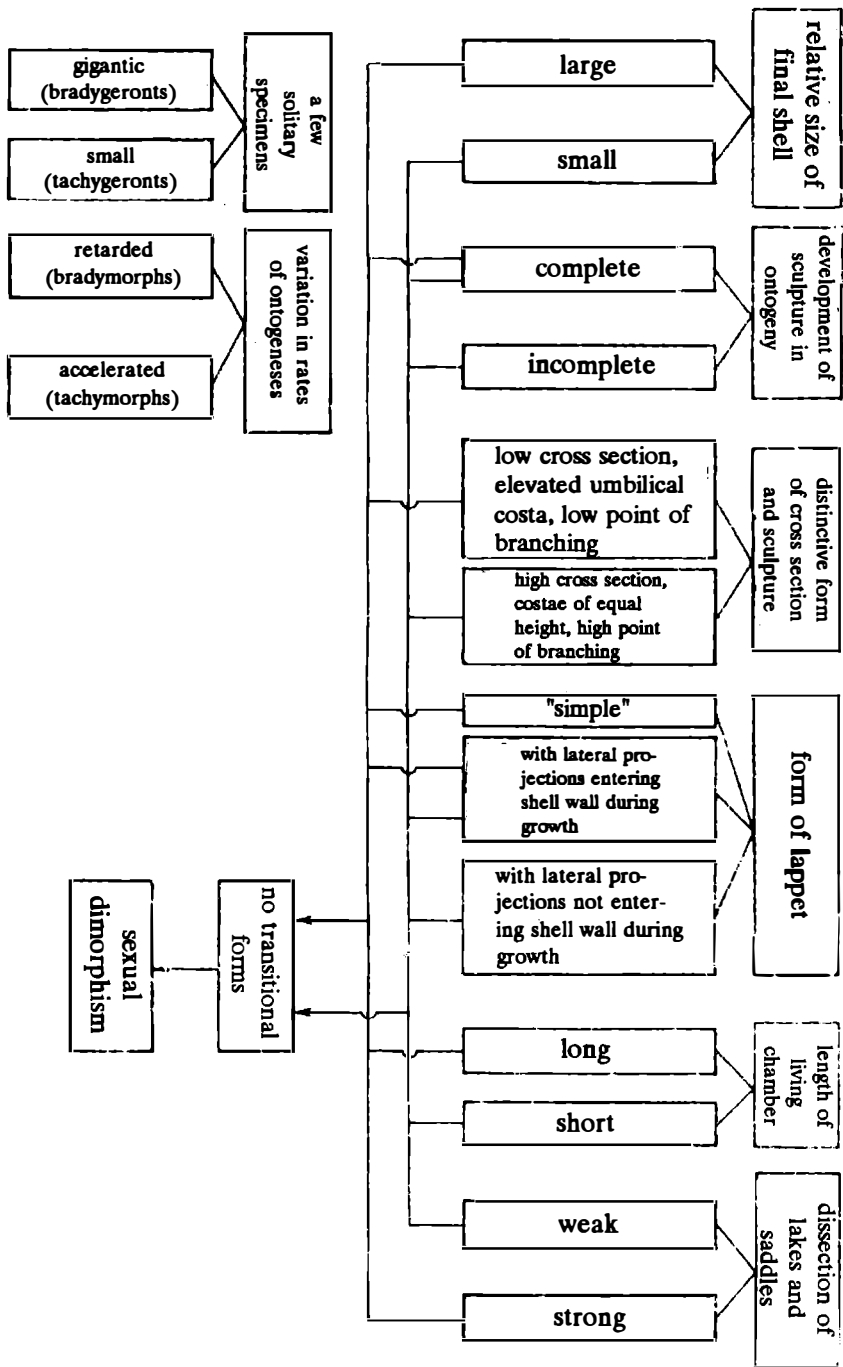


Fig. 1. Intraspecific variation in Jurassic ammonoids.

Polymorphism in the Jurassic ammonoids is manifested in variations and changes in many features: the size and dimensions of the terminal shells (or shells consisting of the same number of whorls), the length of the living chamber, the shape of the aperture, the degree of dissection of the lobes and saddles, the stages in the development of the external sculpture, etc. (fig. 1). The individual features differentiating the morphs are usually correlatively interrelated. This correlation, however, is not always and not necessarily inverse. In assessing the significance of polymorphic features, another aspect of primary importance is their distribution—the presence or absence of transitional forms.

The following three types of intraspecific differences can be distinguished, according to the distribution of characteristics.

Brady- and tachymorphy: Variation in the normal distribution of features expressed as a variation of the rate of morphogenesis of the shell. As a result, in shells of the same size, the extreme end members of a population have features usually more characteristic of earlier whorls (bradymorphic) or, on the contrary, of later stages of development (tachymorphic) than of the intermediate (normomorphic) members of the variability series. Usually manifested in the duration of one or another stage of development of the sculpture. Does not affect the differentiation of dimorphic pairs.

Brady- and tachygeronticity: Variation also characterized by a normal distribution of features. Manifested in the presence of occasionally found shells that differ sharply in size from the other (normogerontic) shells, being two to three times smaller (but with features of the terminal shells)—tachygerontic, or two to three times larger—bradygerontic. Probably associated with some pathology. Because of the rarity of the few solitary finds or for some other reasons, no evidence of dimorphism has been seen in brady- and tachygerontic specimens.

Sexual dimorphism: A stable bimodal distribution of features with no transitional forms of adult shells. This type of polymorphism is the most common, of the greatest interest in taxonomic studies, and will be the subject of further discussion here.

The following types of sexual dimorphs can be discerned in Jurassic ammonoids (fig. 2).

1. Dimorphs differing in shell size.² Such a type of dimorphism has been indicated in the Phylloceratida (Juraphyllitidae) and Ammonitida (Perisphinctina). This kind of dimorphism is the most frequently cited, the hardest to prove and, apparently, the least widespread in its pure form. The shell size usually depends on the number of whorls in combination with the degree of their involuteness; the sculpture is also most often significant in the recognition of dimorphic pairs (Ammonitina, Macrocephalitidae [14]).

2. Dimorphs differing in the shape of the transverse section through their whorls and correlatively associated details of sculpture and degree of involuteness. This is known in some

²Not to be confused with identification of species having very large ("megaconchs" [2, 3]) and very small ("miniconchs" [12]) shells, which are purely adventitious and reflect the variety of living forms of ammonoids.

Dorsoplanitidae, Virgatitidae and Craspeditidae, whose ancestors were characterized by even more sharply expressed dimorphism.

3. Dimorphs differing only in the form of their aperture (correlatively with the growth striation and the inclination of the costae). Such dimorphism is known in the Phylloceratida—Holocophylloceratidae, *Holocophylloceras zignodianum* (d'Orbigny) [1].

4. Dimorphs differing mainly in the size or dimensions of the shell and form of the aperture, and sometimes in the coiling of the living chamber. The macroconchs have an aperture with slight lateral projections and a ventral rostrum, and the configuration of their apertural margin repeats the costation and the growth striation. The microconchs have long lateral projections directed forward and sometimes converging slightly. The traces of projection in smoothed-out form repeat the grown striae. A spiral lateral zone corresponding to the lateral projections sometimes arises—that is, as the shell grows, the projections are incorporated into the composition of its lateral wall. The microconchs also often take on the form of an elliptical cone. Such dimorphism is typical of most genera of Jurassic Haploceratina. The dimorphs cannot be identified on the specific level (unless they are found together, as a rare exception) and are usually combined into subgenera (*Oppelia*—*Oecotraustes*, *Oxycerites*—*Paroecotraustes*, *Lissoceras*—*Microlissoceras*—*Microlissoceras*, *Strigoceras*—*Cadomoceras*).

5. Dimorphs differing in shell size, apertural form, the length of their living chamber and (not always) the degree of development of their sculpture and dissection of their suture line. The macroconchs have an aperture with straight margins, a long living chamber, more strongly dissected lobes and saddles, and an external sculpture that changes more during ontogenesis. Lateral lappets arise periodically and are not incorporated into the shell wall, from which they differ also in sculpture. The lateral lappets often widen at their ends, which converge, almost completely covering the apertural opening so that the latter forms a T-shaped slit, and enfold the ventral side of the preceding whorl. Dimorphs of this type are widely represented in the Perisphinctina (Otoitidae, Stephanoceratidae, Parkinsoniidae, Perisphinctidae, etc.). On the specific level they cannot be identified, and they are usually grouped into subgenera or genera.

6. Dimorphs differing in shell size, apertural form, dissection of the lobes and saddles, and the form of coiling of their whorls to the point of forming heteromorphic shells in the macroconchs. Such dimorphs occur in the Perisphinctina (Spiroceratidae, Morphoceratidae, Tulitidae), and have been regarded as independent genera or subgenera.

The above listing of dimorphs shows that none of the features taken separately, except for the shell size, determines the manifestation of the dimorphism. Dimorphism is differently expressed in various groups of ammonoids, but most often in the differences in structure of the aperture.

It is often thought that the features of dimorphism are manifested in shells that have attained their terminal size. But they can also appear during ontogenesis in the very early growth stages, beginning with the third whorl. The features that can be expressed in ontogenesis are, naturally, limited: the shell size, the apertural projections grown into the shell wall, the stages of development of the sculpture, and the degree of dissection of the suture line (fig. 3); and they may also be masked by their normal development during ontogenesis. The periodic projections of apertures not becoming incorporated into the shell wall are another matter. Traces of them as so-called parabolic ribs and tubercles can be discerned in ontogenesis, beginning with various

stages. If the parabolic ribs appear early (in the third whorl) they are present not only in the microconchs but also in the macroconchs (as in the *Zigzagiceratinae*); if they appear late (at the end of the phragmocone), they can be seen only in the microconchs.

Dimorphism is extremely unevenly distributed in the major taxa of the ammonoids.

In the ancestral group of all the Jurassic ammonoids (the order Phylloceratida), clear dimorphism has been established only in the representatives of the genus *Holocophylloceras* (*Holocophylloceratidae*). Dimorphism of the shell size alone has also been found in some of the *Juraphyllitidae* [10].

Dimorphism is unknown in the order Lytoceratida, if one disregards a determined attempt to combine certain species of the Toarcian *Pachylytoceras* into pairs of dimorphs. The Phylloceratids and Lytoceratids are characterized by extremely great intraspecific variation. Their shells appear to have been cast in the same mold, which is probably due to the predominance of deep-water and partly planktonic forms among them. All the cases of dimorphism, both established and inferred, in these orders occur in lateral lines of ammonoids adapted to a more active hydrodynamic environment.

In the earliest Ammonitida (of the suborder Ammonitina), dimorphism is little developed and is manifested chiefly in the relative size of the shell. Apertures with lateral projections begin to form in the family Hildoceratidae, which gave rise to the latter suborder Haploceratina. Dimorphism is most characteristic of two suborders of the Ammonitida: in the Haploceratina the microconchs bear lateral projections that become grown into the shell wall, and in the Perisphinctina they have periodic lateral lappets.

Dimorphism develops differently in the phylogenesis of short lines. In the suborder Haploceratina, at least the Jurassic, dimorphism is a constant feature, and the forms of its manifestation are quite stable and can be easily derived from the ancestral monomorphic shells. In the suborder Perisphinctina, dimorphism may disappear in the short evolutionary series (the Parkinsoniidae) (fig. 4) or else be substantially modified. The form of the aperture with lateral lappets cannot be derived from ancestral forms, but seems to have appeared very suddenly.

A definite correlation can probably be discerned between the types of manifestation of dimorphism and the types of aptychi. Aptychi are characteristic of taxa in which dimorphism does not occur at all or is manifested only in the size of the shells (the Lytoceratida and the older Ammonitina: *Psiloceratidae*, *Arietitidae*, *Liparoceratidae*, *Amaltheidae*).

Diptychi of the type of *Cornaptychus*, *Lamellaptychus*, *Laevilamellaptychus*, and *Punctaptychus* are typical of the late Ammonitina with an aperture having slight lateral projections (the Hildoceratidae), and of the suborder Haploceratina with microconchs having apertures with long lateral projections grown into the shell wall.

The various kinds of dimorphism that have microconchs with apertures having lateral projections can also be correlated with the living forms of the shells. Lateral projections grown into the shell wall are typical predominantly of smooth or slightly sculptured oxycones, ellipticones, and platycones—that is, shell forms traditionally regarded as pelagic. Periodic lateral lappets can be seen on strongly sculptured serpenticones and forms intermediate between

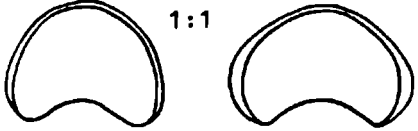
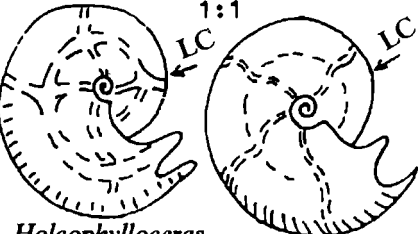
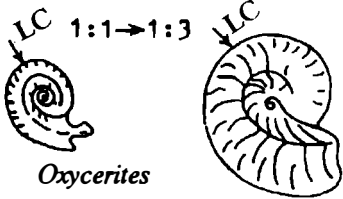
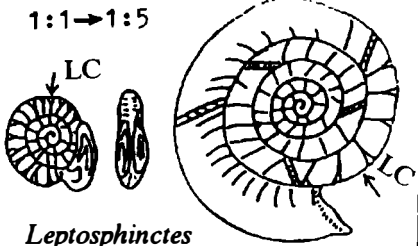
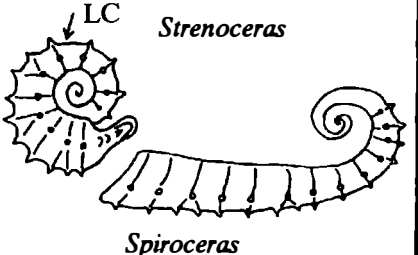
Differences between dimorphs	Distribution by taxa	Remarks and illustrations
in shell size	Juraphyllitidae Perisphinctina	most often mentioned and least proven type of dimorphism
in form of cross section, details of sculpture and degree of involuteness	Virgatitidae Dorsoplanitidae Craspeditidae	 <i>Lomonossovella</i>
in form of lappet	Holcophylloceratinae	 <i>Holcophylloceras</i>
in form of lappet and in shell size, evoluteness of living chamber	Oppeliidae Strigoceratidae Lissoceratidae Haploceratidae	 <i>Oxyerites</i>
in form of lappet, shell size, development of sculpture, dissection of suture line, and length of living chamber	Otoitidae Stephanoceratidae Kosmoceratidae Parkinsoniidae Reineckiiidae Aspidoceratidae	 <i>Leptosphinctes</i>
in form of lappets; one of dimorphs acquires heteromorphic shell	Spiroceratidae	 <i>Srenoceras</i> <i>Spiroceras</i>

Fig. 2. Types of dimorphism in Jurassic ammonoids; lc - living chamber, with arrow marking its beginning.

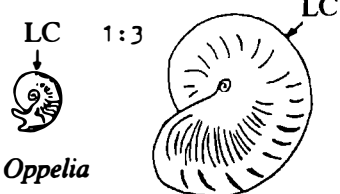
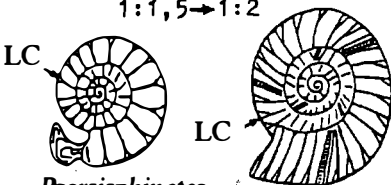
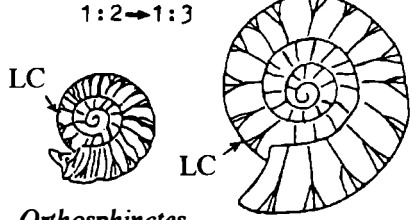
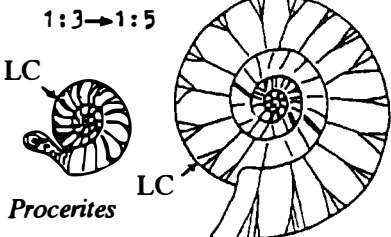
Particular dimorphic features	Illustrations and ratios of dimorphs
projections of apertural margin turn into shell and become fixed by growth striae and changes in wall thickness	 <p style="text-align: center;">LC 1:3 LC</p> <p style="text-align: center;"><i>Oppelia</i></p>
no signs of lateral lappets visible on microconchs	 <p style="text-align: center;">1:1,5 → 1:2</p> <p style="text-align: center;">LC LC</p> <p style="text-align: center;"><i>Prorsisphinctes</i></p>
traces of lateral lappets of microconchs manifested as constrictions, parabolic costae, and tubercles on inner whorls	 <p style="text-align: center;">1:2 → 1:3</p> <p style="text-align: center;">LC LC</p> <p style="text-align: center;"><i>Orthosphinctes</i></p>
constrictions and traces of lateral lappets in form of parabolic costae on inner whorls of micro- and macroconchs	 <p style="text-align: center;">1:3 → 1:5</p> <p style="text-align: center;">LC LC</p> <p style="text-align: center;"><i>Procerites</i></p>

Fig. 3. Development of dimorphic features in ontogenesis; for legend, see Fig. 2.

serpenticones and cadicones, including eccentric ones, which with some justification are regarded as bottom-dwellers in shallow waters.

The various types of dimorphism can probably be differently interpreted in terms of their biological function and their belonging to one sex or the other. At any rate, the commonly accepted assignment of the macroconchs to males and the microconchs to females can hardly be supported, since the shell size did not always reflect the size of the living organism, and the question of the functional significance of the various shapes of aperture has more than one answer.

It is evident that the lateral projections of the aperture, which were grown into the shell wall and

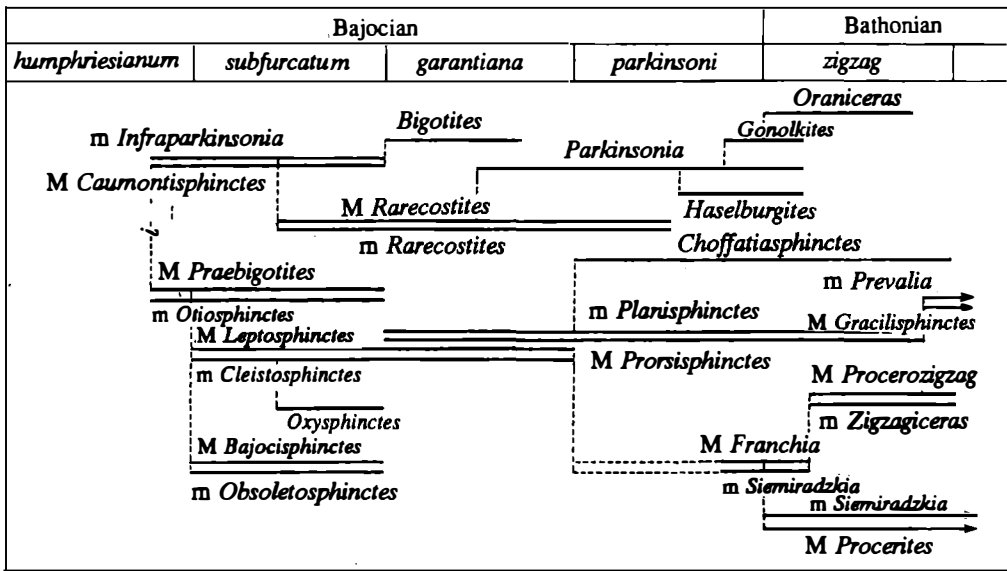


Fig. 4. Evolution of certain Middle Jurassic Perisphinctina.

like it formed the anterior margin and outer surface of the mantle, were external relative to the soft body that extended beyond the shell aperture. With living chambers of the same length and shells of the same size, as in *Holcophylloceras*, the organism with features of the microconch was larger in its aperture. In the Haploceratina the relative (in terms of fractions of a whorl) length of the living chamber of the macro- and microconchs was approximately the same, but the macro- and microconchs differed substantially in absolute shell size (1:3). The length of their lateral lappets may reach 1/5 of a whorl—that is, this increment does not compensate the difference in size. On the other hand, the great extent of the lappets, sometimes exceeding half the length of the living chamber, shows that a considerable part of the soft body of the microconchs was outside the shell and could hardly have retracted into it.

The lateral lappets on the microconchs of the Perisphinctina (fig. 5) may reach 1/4 of a whorl in length, almost completely enveloping the preceding whorl on both sides (the shells being evolute, on the whole), covering the apertural opening, and differing sharply in sculpture from the shell wall (the sculpture of the lateral lappets in the Perisphinctina is closest to the striate sculpture of the aptychi, but the microstructure of the lappets has not been investigated). It is also important that the margin of the outer ends of the lappets may project far beyond the general contour of the cross section through the shell.

What function could the such lappets have served? Since their ends were pressed against the ventral side of the preceding whorl, they could not have served as a support for organs located within the shell. And since they form a narrow, often fissure-like aperture, they could hardly have served as a constant frame for the living mouth.

Thus, the apparent lack of logical purpose of the lateral lappets in the Perisphinctina as elements of the external shell is evident. The alternative interpretation—lappets as an element

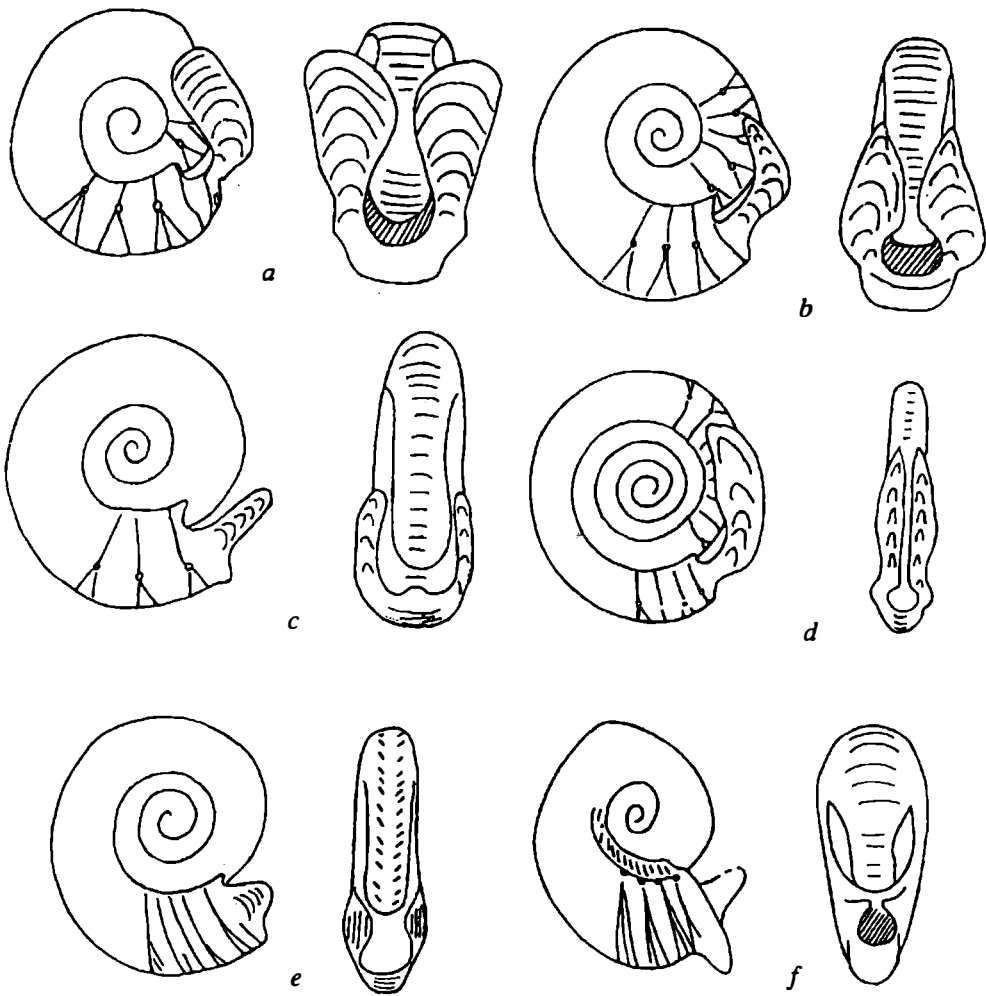


Fig. 5. Different shapes of apertures in microconchs of Perisphinctina: *a* - *Itinsaites* (Early Bajocian), *b* - *Normannites* (Early Bajocian), *c* - *Polyplectites* (Late Bajocian-Bathonian), *d* - *Leptosphinctes*, *Praebigotites*, and *Procerites* (Late Bajocian-Bathonian), *e* - *Rarecostites* (Late Bajocian), *f* - *Bullatimorphites* (Middle to Late Bathonian).

of the internal skeleton—seems preferable, but also raises questions. Although their resemblance to aptychi in sculpture and color is quite clear, they can hardly be considered an element of the buccal apparatus, since cases are known (not many, to be sure) of the occurrence of aptychi in the living chambers of microconchs with lappets (*Strenoceras*, *Normannites*).

If the lateral lappets were supports for the attachment of musculature, what were these muscles? A specimen of *Otiosphinctes irganajensis* with well-developed lappets has, on the cast of its living chamber, impressions of retractors approaching the ventral parts of the sides, and the necessary ventral divergence of the lappets most likely served as an aperture for the emergence of the hyponome—that is, the supporting function of these lappets may have applied only to the head part of the soft body.

Another indirect argument in favor of the internal position of the lappets on the microconchs of *Perisphinctina* may be the clearly observable fact of the considerably lesser variety of the shells of the microconchs in comparison to the parallelism of the macroconchs (if the microconchs are taken to be the males, this contradicts the well-known rule that the females are more conservative in regard to their variation; but on the assumption of the external position of part of the soft body of the microconch ammonite, this contradiction can be eliminated: the microconch is a quasi-rudiment of the shell that with equal degree of likelihood may have belonged to either a male or a female).

It should be noted, finally, that when the lateral lappets are lost in the course of phylogenesis, what one observes is their reduction and not their abrupt separation from the shell—that is, they are not transformed into an independent element of the skeleton.

The following conclusions are suggested by the above facts.

1. Polymorphism in the Jurassic ammonoids is manifested in three basic types of intraspecific differences: brady- and tachymorphism, brady- and tachygeronticity, and sexual dimorphism.

2. Dimorphism of the shells is widespread in the Jurassic ammonoids. The forms of its occurrence and the manifestations of the differences in dimorphic pairs vary extremely widely, but are characteristic of taxa of higher rank. The orders *Lytoceratida* and *Phylloceratida* show no dimorphism, or else it appears only in differences in size, and only in one family of phylloceratids in the form of the aperture. In the suborder *Ammonitina* as well, dimorphism does not appear or is manifested only in size differences (in the late *Hildoceratidae* like the dimorphism in their descendants). In the suborder *Haploceratina*, by contrast, dimorphism is almost constantly observable, and is manifested in shell size and in the formation, in the microconchs, of external lateral lappets that are grown into the shell wall. In the suborder *Perisphinctina*, dimorphism is primary; it may disappear in the course of phylogenesis of individual lines and be manifested in the size of the shell, length of the living chamber, and the formation, in the microconchs, of internal lateral lappets that are not grown into the shell wall.

3. The differences in manifestation of dimorphism probably reflected the different functions of the dimorphic features. Although in its nature dimorphism, as it is manifested in the Jurassic ammonoids, must be considered sexual, the dimorphs can be only arbitrarily assigned to a particular sex. This assignment can be made more confidently if the functions of the dimorphic features are ascertained.

4. The acknowledgement and acceptance of dimorphism give rise to certain nomenclatural problems, which can, however, be successfully solved. We must not only try to achieve the necessary combination of taxa of specific and generic rank, in which their diagnoses will be lost or become invalidated—that is, the dimorphism must also be reflected in the nomenclature. The following versions are possible, depending on the degree to which dimorphism is manifested:

(a) The combination of morphs on the level of species with an indication of the morphs when, in the absence of preserved features of the dimorphs, the shells become hard to distinguish (for example, *Rarecostites*, and also dimorphs distinguishable only by their size). This variant is appropriate when the dimorphic features have no substantial effect on the identification of species or the diagnoses of higher taxa (for example, the Volgian *Virgatitidae*, *Dorsoplanitidae*, and *Craspeditidae*):

(b) The grouping of the dimorphs into subgenera and their combination within the composition of one genus when the members of the dimorphic pairs form parallel evolutionary series. However, certain difficulties arise here that are associated with the different types of manifestation of the new characters in the macro- and microconchs in one line. Since the latter are more conservative, the microconch subgenus may have to be broken down into two macroconch subgenera (*M Franchia*, *M Procerites*, m *Siemiradzkaia*), with strongly divergent characters within one generic grouping, resulting in the appearance of many subgenera of both M and m:

(c) Retention of the genera with one of the leading features of the dimorphs—that is, usually the microconch genera, in the absence of any reliable correlation with the macroconch genus (as with *Stenoceras*).

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