SYSTEMATICS, AFFINITIES, AND LIFE HABITS OF *BABINKA*, A TRANSITIONAL ORDOVICIAN LUCINOID BIVALVE

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ABSTRACT. The rare bivalve genus *Babinka* from lowest Middle Ordovician rocks of the Bohemian Basin shows multiple muscle scars which have led several palaeontologists to suggest a relationship to some metameric molluscan ancestor. A systematic and morphologic revision reveals that *Babinka* is a typical bivalve in all features except the pedal and gill muscle-scar patterns. These scars are not like those of other bivalves, but are almost identical to the pattern found in the recent monoplacophoran *Neopilina*, and in some early Palaeozoic Monoplacophora. This close similarity confirms the suggestion that the muscle pattern in *Babinka* is an inheritance from a monoplacophora-like ancestral mollusc.

Babinka is among the first bivalves to appear in the fossil record. The genus is both chronologically and morphologically an ideal ancestor for the earliest lucinoid bivalves which appear abruptly in Middle Silurian deposits. Morphological features of *Babinka* which are strongly suggestive of lucinoid affinities are: the anteriorly-expanded shell shape; the elongate anterior adductor muscle with associated 'elongate impression'; the non-sinuate pallial line; and the typical lucinoid hinge, dentition, and ligament. *Babinka* provides the first direct evidence of an evolutionary transition between the Bivalvia and more primitive molluscs.

Functional comparison with recent lucinoid bivalves suggests that *Babinka* was a mobile, infaunal suspension feeder that received nutrient-laden water into the mantle cavity through an anterior inhalent opening maintained by extrusion of the foot.

SEVERAL students of molluscan phylogeny have recently called attention to the curious early bivalve genus *Babinka* (Barrande, 1881) from Ordovician rocks of Czechoslovakia. This rare monotypic genus is known only from the Bohemian Basin where it occurs in a formation (Šárka beds) that is probably of Llanvirn (lowest Middle Ordovician) age. Bivalve molluscs are extremely rare in Llanvirn or pre-Llanvirn rocks, and for this reason alone *Babinka* is of particular interest as one of the first known representatives of the Bivalvia. Further interest attaches to the genus because internal moulds preserve clear impressions of multiple pairs of muscle scars. These multiple muscle scars have led to the suggestion that *Babinka* is a primitive transitional form between the Bivalvia and some metameric molluscan ancestor (Vokes, 1954; Cox, 1959, 1960; Růžička and Prantl, 1960; Horný, 1960; Vogel, 1962; Merklin, 1962).

Although *Babinka* has been the source of much speculation regarding the early history of the Bivalvia, the genus has not been critically restudied since its first cursory description by Barrande almost a century ago. While preparing a review of the phylogeny and adaptations of Palaeozoic lucinoid bivalves, I have noted many characters of *Babinka* that suggest a relationship to the first lucinoid forms which appear abruptly in Middle Silurian deposits. The present study was prompted by this possibility of lucinoid affinities, and by the often suggested transitional evolutionary position of the genus. This paper has been prepared in order to: (1) review the systematics and morphology of *Babinka*; (2) further examine the functional and phylogenetic significance of the muscle scar pattern and other morphologic features of the genus; (3) suggest that *Babinka* is an ancestral lucinoid bivalve, and; (4) attempt to interpret the life habits of *Babinka* by analogy with recent lucinoid forms. More general phylogenetic and systematic

conclusions which have resulted from the study will be treated in a separate paper (McAlester, 1965).

BABINKA AS A PRIMITIVE BIVALVE

Vokes (1954) appears to have been the first to call attention to the possible phylogenetic significance of the muscle scars in *Babinka*. He noted that the multiple scars of the genus, and the dissimilar multiple muscle scars of several Ordovician nuculoid species, are suggestive of the series of pedal muscle scars seen in fossil monoplacophorans, and he concluded (p. 236): '. . . the muscle scars shown by these Ordovician pelecypods can be shown to be close to those exhibited by primitive gastropods . . . they therefore may be interpreted as reflecting the musculature present in the ancestral stock from which the Pelecypoda were derived. Further, they suggest that the adductor muscles of the Pelecypoda are derived from discrete pairs of the ancestral musculature, rather than from the union of multiple pairs.'

Vokes suggestion was discussed by Cox (1959, 1960), who agreed in concluding (1959, p. 204) that *Babinka* 'could well have been newly evolved from the ancestral mollusc'. Cox further noted (1960, p. 71) that '*Babinka* appears to have approximated to the theoretical concept of the newly evolved bivalve mollusc. Little can be said about the role it played in bivalve phylogeny until it is better known.'

The idea that *Babinka* might be closely related to a monoplucophora-like ancestor was repeated by Růžička and Prantl (1960), and greatly expanded by Horný (1960), who regarded the genus as 'the phylogenetically initial form of the pelecypods' (p. 479). Because of this proposed phylogenetic position, Horný erected a new family (Babinkidae) and order (Diplacophora) for the genus. The latest discussions are those of Vogel (1962) and Merklin (1962), both of whom agree with Horný's conclusions.

Barrande's original descriptions, and all later discussions of *Babinka*, have not clearly established the nature and number of the multiple muscle scars which have aroused so much interest. In an attempt to clarify the generic morphology, I have restudied all specimens of *Babinka* in North American museums, and in the Národni Muzeum at Prague (see the section on Systematics, p. 241). This revision has provided several natural internal moulds which reveal for the first time the fine details of the muscle impressions. Of particular importance in showing the precise pattern is one extraordinarily clear internal mould of a right valve from the collections of the Národni Muzeum which was generously made available for study by Dr. Horný (Pl. 28, figs. 9–11). These internal moulds show that *Babinka* has normal adductor muscle scars (text-fig. 1, aam, pam) and, in addition, a series of eight smaller scars above and between the adductor impressions. To avoid functional connotations, these eight scars will be temporarily referred to as the 'intermediate' muscle-scar impressions (text-fig. 1, im). Below some of these intermediate impressions is a series of about twenty-five still smaller scars. These will be temporarily called the 'small' muscle-scar impressions (text-fig. 1, sm). Finally, a large but obscure and faintly bounded 'elongate impression' (text-fig. 1, ei) extends ventrally from the anterior adductor scar, and a faint non-sinuate pallial line of mantle muscle attachment connects the adductors in the usual position (text-fig. 1, pl).

The first problem in interpreting the muscle scars of *Babinka* concerns the cross-sectional shape of the muscles which attached to the adductor, 'intermediate', and 'small' scars. On well-preserved internal moulds these three groups of scars are strongest

in sharply raised areas at their ventral extremities (the raised areas on the internal moulds represent strong depressions on the original shell interior). Extending dorsally from the raised extremities are more faintly raised 'tails', which converge toward the umbonal region (text-fig. 1). These 'tails' are the traces of the position of the muscle scars at earlier stages of growth. In most bivalves the earlier muscle attachment sites are completely obscured by later deposition of inner shell material, but in *Babinka* this later deposition was not thick enough to cover completely the earlier trace of the muscle scars. Some workers have assumed that muscles attached along the entire elongate impression, but it is now apparent that the functional muscle at any one time occupied
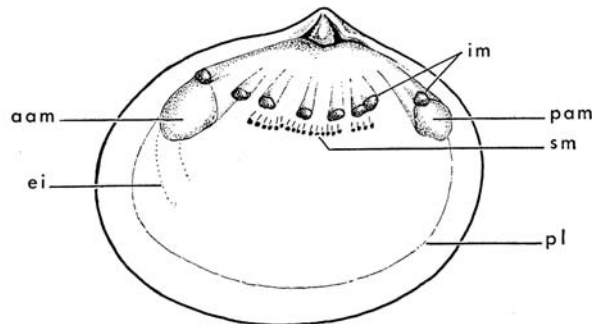
TEXT-FIG. 1. Muscle-scar pattern in *Babinka*, aam, anterior adductor muscle scar; ei, 'elongate impression'; im, 'intermediate' (pedal) muscle scars; pam, posterior adductor muscle scar; pl, pallial line; sm, 'small' (gill) muscle scars.

only the ventral extremity of each impression. The shape of the strongly raised extremities show that only the anterior adductor muscle was somewhat elongate in life. The muscles which attached to the posterior adductor scar and to all of the 'intermediate' and 'small' scars were approximately round in cross-section.

The two largest muscle scars in *Babinka* occupy anterior and posterior marginal positions along the line of pallial attachment, as do the adductor muscles in all isomyarian bivalves, and there is no reason to doubt that they are the attachment sites of typical isomyarian adductor muscles. The function of the muscles which attached to the 'intermediate' and 'small' scars is more problematical.

The intermediate scars were considered by Barrande, Vokes, and Horný to represent the attachment sites of the pedal musculature. All recent isomyarian bivalves have paired pedal muscles, with one muscle of each pair attaching to each valve (text-fig. 2). These muscles commonly leave distinct shell impressions. In many recent isomyarian bivalves the foot is anchored by only two strong pairs which attach immediately above the adductor muscles (text-fig. 2; *Crassatella, Codakia, Mercenaria, Tellina*). Other groups have additional strong pedal muscle pairs which attach and leave scars in the central dorsal region. Living *Nuculana* and related protobranch forms commonly have five or six pairs of pedal muscles (text-fig. 2, *Nuculana*), some living Cardiacea have three strong pairs (text-fig. 2, *Cardium*), and some Mactracea have as many as five pairs

(text-fig. 2, *Mesodesma*). Recent isomyarian bivalves thus show considerable variation in the number of pedal muscle pairs. Normally only two strong pairs attach above the adductor muscles, but in several unrelated groups there are from one to four additional pairs between the two principal pairs.

The 'intermediate' muscle scars of *Babinka* are similar in size and position to the pedal scars of recent isomyarian bivalves. As in recent forms, two pairs of pedal muscles attach directly above the adductors. The six additional pairs of muscles between the adductors in *Babinka* are almost certainly analogous to the additional strong pedal
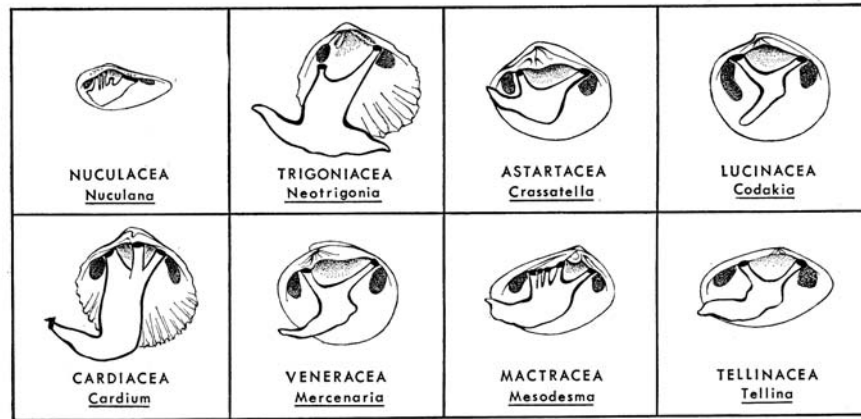

TEXT-FIG. 2. Pedal musculature of genera representing eight superfamilies of recent isomyarian bivalves. Pedal-attachment sites shown for right valves only. The pattern is repeated in the left valves making symmetrical right–left pairs of pedal muscles. Note the presence of 3 to 5 pedal attachment sites in *Nuculana*, *Cardium*, and *Mesodesma*. Data from Allen, 1958; Heath, 1937; Pelseneer, 1891, 1911; Yonge, 1939, 1949.

muscle pairs found in several unrelated recent superfamilies. These similarities strongly suggest that the 'intermediate' muscle scars of *Babinka* do in fact represent the attachment sites of pedal muscle pairs.

The pedal muscles of bivalves have completely different functions than do the adductor muscles, and it is most probable that the two kinds of muscles had separate evolutionary origins. Because both the pedal and adductor impressions in *Babinka* show a similar elongate shape, there has been a tendency to assume that the large adductors represent two additional pairs of pedal muscles which have become hypertrophied. It is much more likely, however, that the adductor muscles of the Bivalvia did not originate from modification of the pedal musculature, but instead arose independently by cross-fusion of the pallial attachment muscles, as has been convincingly stressed in the writings of Yonge (1953, 1957). If this reasonable conclusion is correct, then the adductor muscles in *Babinka* cannot be considered to represent additional pairs of modified pedal muscles.

The 'small' muscle scars and the faint 'elongate impression' have not been previously recognized in *Babinka*, and it is the 'intermediate' muscle scars (which will hereafter be

termed the 'pedal muscle scars') which have led to the repeated suggestion that *Babinka* is related to some metameric ancestral mollusc. Similar multiple pairs of pedal muscles occur in several unrelated and divergently specialized groups of recent bivalves, and it is therefore evident that the mere presence of such muscles does not indicate a primitive condition. A strong suggestion of primitiveness is seen, however, from comparing the pattern of pedal and 'small' muscle scars in *Babinka* with the muscle attachment pattern
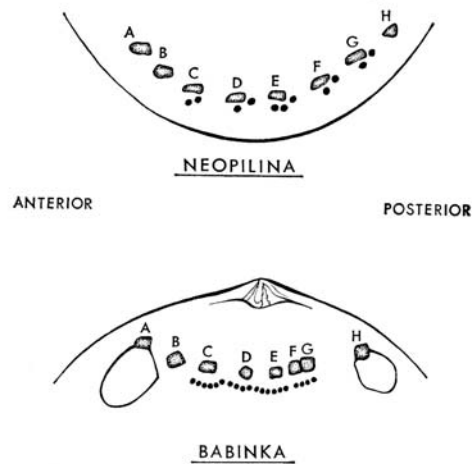
TEXT-FIG. 3. Comparison of muscle-scar patterns in *Babinka* and the recent monoplacophoran *Neopilina*. A–H, Eight pairs of principal pedal muscles. The small dots below the pedal muscles show the position of gill attachment muscles in *Neopilina*, and the position of the 'small' muscle scars in *Babinka*. Data on *Neopilina* from Lemche and Wingstrand, 1959.

of *Neopilina*, the only recent representative of the primitive molluscan Class Monoplacophora.

Lemche and Wingstrand have provided detailed descriptions of the pattern of muscle attachment to the shell of *Neopilina galatheae*; in that species the foot and visceral mass attach by eight strong pairs of pedal muscles (Lemche and Wingstrand, 1959, figs. 120, 121, 130). Associated with these eight pedal muscle pairs are a series of much smaller muscles having various functions, including pallial, ctenidial, radular, and visceral muscles. Among the strongest of these small muscles are the ctenidial muscles, which serve to attach the gills to the shell. *N. galatheae* has five pairs of gills which attach to the shell by many small muscles situated around the third through seventh pairs of larger pedal muscles (text-fig. 3).

Lemche and Wingstrand (1959, fig. 133) note that the muscle pattern in *N. galatheae* is closely analogous to the strong muscle-scar pattern of the Silurian monoplacophoran genus *Pilina*. Like *Neopilina*, this early fossil probably had eight strong pairs of pedal muscles and associated smaller ctenidial, radular, pallial, and visceral muscles.

This eight-paired pattern is not universal in the Monoplacophora, for some other early Palaeozoic genera show fewer than eight pedal muscle pairs. It may be significant, however, that eight appears to be the maximum number of pedal muscle pairs found in any monoplacophoran, and in some species the smaller number of pedal scars appear to have resulted from fusion of originally more numerous pairs.

The pattern of pedal and 'small' muscle scars in *Babinka* shows an amazing similarity to the pattern of pedal and ctenidial muscle attachment in *Neopilina* (text-fig. 3). As in *Neopilina*, *Babinka* has eight pairs of pedal muscle scars. Even more strikingly, the 'small' muscle scars of *Babinka* occur under the third to seventh pairs of larger pedal muscle scars in the same position as the ctenidial attachment muscles in *N. galatheae*. Although it is tempting to draw immediate phylogenetic conclusions from these similarities, several facts suggest that the relationships may not be as simple as they first appear.

First, the detailed pattern of muscle impressions in *Babinka* is clearly visible on only one unusually well-preserved internal mould of a right valve from the collections of the National Museum at Prague (Plate 28, figs. 9–11). This is the only specimen which shows the 'small' muscle scars and all eight pedal muscle scars. The central pairs of pedal scars are preserved on many specimens, and these have been the source of the previous speculation regarding the muscle-scar pattern of the genus. A few specimens also preserve either the anterior or posterior pedal scar above the adductors, but only the single Prague specimen clearly preserves all eight pairs. It is therefore impossible to fully evaluate the variability in number and position of the pedal and 'small' muscle scars. Composite evidence from many specimens suggests a reasonably constant pedal muscle pattern, but the variability of the 'small' muscles is completely unknown.

Further difficulties are raised by the presence of fewer than eight pedal muscle pairs in many fossil monoplacophorans, and also by the occurrence of six instead of five gill pairs in a second recent species of *Neopilina*, *N. ewingi* Clarke and Menzies (1959). The anatomical details of this species have not yet been described, but it is probable that it has a somewhat different pattern of gill muscle attachment than does *N. galatheae*. In spite of these cautions and qualifications, I feel that the muscle patterns in *Neopilina*, *Babinka*, and some early fossil monoplacophorans are too similar to be entirely the result of chance, and I believe it is reasonable to infer that the pedal and 'small' muscle scars in *Babinka* do in fact represent an inheritance from some monoplacophora-like ancestor. It will be stressed later that in all features except the pedal and 'small' muscles, *Babinka* is a typical representative of the Class Bivalvia.

Implicit in the above comparisons is the suggestion that the 'small' muscle scars in *Babinka* represent the site of attachment of the gills. This possibility is raised not only by the similar position of these scars and the gill muscles of *Neopilina*, but also by the observation that no other large organs are likely to have been attached to the shell in the position of the 'small' scars. Direct gill attachment to the shell by many small muscles has no obvious analogue in recent bivalves, but the position of the scars in *Babinka* is geometrically correct to have supported a ctenidial structure in the mantle cavity. In addition, the many separate pedal scars of *Babinka* suggest that the animal still lacked the united pedal-visceral muscle system which supports the gills in most recent bivalves. A strong direct attachment of the gills to the shell may therefore have still been necessary. It is most probable that the 'small' scars were the sites of gill attachment, and they

will henceforth be referred to as the 'gill muscle scars'. The many small muscles which attached to these scars may have supported a single large gill or, less probably, they might represent the attachment sites of several small gills.

The two final internal scars preserved in *Babinka* are the non-sinuate pallial line, and the faint 'elongate impression' below the anterior adductor. Both of these features suggest a relationship between *Babinka* and the bivalve Superfamily Lucinacea, and they will be considered in detail in the next section.

BABINKA AS AN ANCESTRAL LUCINOID BIVALVE

The oldest undoubted lucinoid bivalves are found in Middle and Upper Silurian limestones on the island of Gotland, Sweden. Two lucinoid species are found in abundance in the Gotland deposits (Hede, 1921; Munthe *et al.*, 1925; Haffer, 1959). One species, for which the correct name is probably *Paracyclas hisingeri* (Murchison and Verneuil), is a small, rounded, inflated form which is similar in shape to recent species of the lucinoid family Diplodontidae. The other Gotland species, *Ilionia prisca* (Hisinger), is a much larger, compressed form which closely resembles some recent species of the family Lucinidae. The internal morphology of *P. hisingeri* is poorly known, but the larger species, *I. prisca*, is found principally as internal moulds which preserve some muscle scar impressions. All of the morphologic features of *I. prisca* are strongly characteristic of recent Lucinacea (Allen, 1958). Among the similarities are: an extremely elongate anterior adductor muscle; an unusual anteriorly-expanded shell shape; and a unique radial shell groove near the dorsal valve margin which corresponds to the internal line of attachment of the gill to the visceral mass. The presence of these distinctive lucinoid characteristics in *I. prisca* makes it extremely probable that the species is closely related to recent Lucinacea. This superfamily was therefore fully established in mid-Silurian time. The group has a scattered but continuous fossil record after the Silurian, and is represented in modern oceans by about two dozen genera which are usually assigned to three families. This abrupt appearance of fully developed and essentially modern lucinoid bivalves in Middle Silurian deposits indicates that the group must have had a considerable evolutionary history before the Silurian, but as yet no possible ancestral or related fossil forms have been recognized in older deposits. Many morphologic features of *Babinka* strongly suggest lucinoid affinities and these, coupled with its occurrence in Middle Ordovician rocks, make it both morphologically and stratigraphically an ideal ancestor for such Silurian lucinoids as *Ilionia*. The morphologic features of *Babinka* which are strongly suggestive of lucinoid affinities are: (1) the characteristic anteriorly expanded shell shape, (2) the elongate anterior adductor muscle scar and associated 'elongate impression', (3) the simple, non-sinuate pallial line, and (4) the typical lucinoid hinge, dentition, and ligament. In short, the only features of *Babinka* which are not typically lucinoid are the primitive patterns of pedal and gill muscle scars.

Comprehensive studies of living Lucinacea (Allen, 1958, 1960) have shown that the characteristic anteriorly-extended shape and elongate anterior adductor muscle are related to an unusual mode of life found in all recent representatives of the group. Instead of drawing respiratory and feeding currents into the mantle cavity through posterior siphons, as do most deeply buried infaunal bivalves, the Lucinacea construct a unique mucous-lined, anterior inhalent tube in the surrounding sediment by means of

the elongate, cylindrical foot. The characteristic elongate anterior adductor muscle is directly related to this habit for the solid outer face of the muscle is ciliate and serves as a preliminary sorting area for food particles brought in by the anterior inhalent current (text-fig. 4). This unusual habit is universal in living lucinoids, and was almost certainly shared by Silurian and Devonian lucinoids which show the characteristic elongate anterior adductor scar.

The anteriorly expanded, flattened shell of *Babinka* is similar in shape to the Silurian
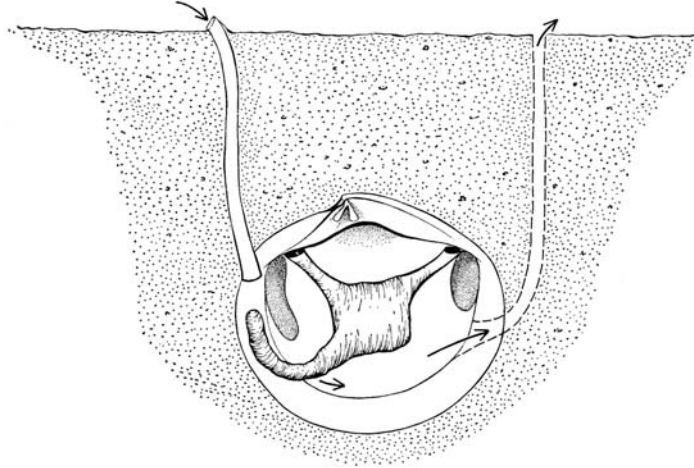
TEXT-FIG. 4. Life position of recent lucinacean bivalves (modified from Allen, 1958). Nutrient-laden water is brought into the mantle cavity through a mucous-lined anterior inhalent tube constructed by the foot. In some genera the posterior exhalent current discharges directly into the sediment, in others it is channelled to the sediment surface through a retractable posterior siphon. The anterior face of the elongate anterior adductor muscle is covered with cilia and acts as a preliminary sorting area for incoming food particles.

species *I. prisca* (text-fig. 5; Pl. 27, figs, 6, 7). Even more suggestive is the pattern of the anterior adductor muscle and associated 'elongate impression' in *Babinka*. The anterior adductor scar of *Babinka* is considerably more elongate in a radial direction than is the posterior scar, although it does not yet show the extreme ventral elongation seen in *Ilionia* and most younger lucinoids. The radial elongation of this muscle in *Babinka* does, however, suggest the beginning of a trend toward increasing the surface area of the anterior adductor. Furthermore, several internal moulds of *Babinka* show a faint 'elongate impression' marking the site of an obscurely bounded depression extending ventrally from the anterior adductor on the original shell interior. This 'elongate impression' has exactly the same shape and position as the elongate anterior adductor muscle scar in *Ilionia* and most other lucinoids (text-fig. 5; Pl. 28, figs. 10, 12). The impression is too faint to represent an expansion of the actual adductor muscle, but it does indicate that there was some differentiation and specialization of the mantle in the region below the anterior adductor in *Babinka*. The 'elongate impression' might
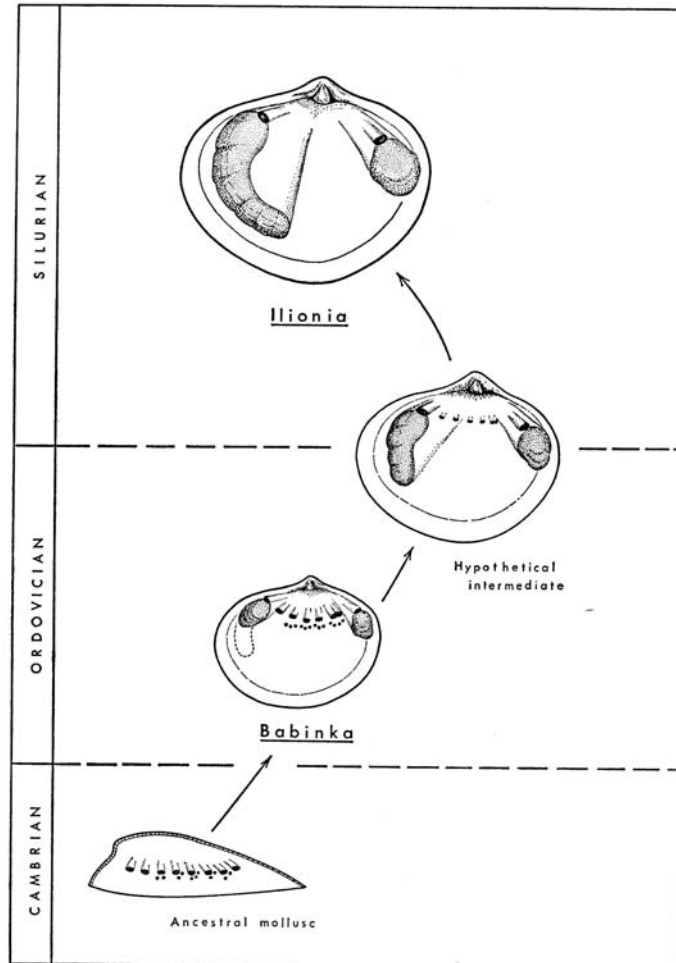
TEXT-FIG. 5. Proposed evolutionary relations of *Babinka*. Note the progressive
reduction of the pedal muscles and the expansion of the anterior adductor
muscle between *Babinka* and *Ilionia*.

reasonably represent the attachment surface of some kind of specialized ciliary sorting
area which was similar in position and function to the elongate adductor muscle surface
in later lucinoids. This sorting area would probably not have formed a connected parti-
tion between the valves and would have been less efficient than the sorting tube formed
by the solid face of an elongate adductor muscle. It is not difficult, therefore, to visualize

an evolutionary progression between *Babinka* and *Ilionia* involving an expansion of the adductor into the position of the 'elongage impression'. It is also worth noting that *Ilionia* shows a rounded posterior adductor scar with an elongate trace of the earlier growth position which is almost identical to that of *Babinka* (text-fig. 5). Regrettably, all of the internal moulds of *Ilionia* available for comparison in the Yale Peabody Museum collections are too poorly preserved to show the details of the pedal muscle scars, but the genus most probably had the typical lucinoid pattern with one pair of strong pedal muscles above each adductor.

Because of the anterior inhalent tube and consequent absence of a posterior inhalent siphon, the Lucinacea are unusual among deeply buried infaunal bivalves in lacking a pallial sinus for siphon retraction. Some recent lucinoids do have a small posterior *exhalent* siphon, but this single siphon is retracted by a unique inside-out inversion which does not require an indentation in the line of pallial muscle attachment. True lucinoid bivalves all lack a pallial sinus, and it is suggestive that *Babinka* also shows a non-sinuate line of pallial muscle attachment.

In many fossil and recent lucinoid species the hinge teeth are poorly developed or absent, but when present the dentition consists of a large, commonly lobed, cardinal tooth in the right valve fitting between two smaller teeth in the left valve (Pl. 28, figs. 5–8; Allen, 1960; Chavan, 1937–8, 1962). In some genera lateral teeth and an additional small cardinal tooth in the right valve are added to this basic pattern. Several internal moulds of *Babinka* preserve impressions of the dentition, and latex casts of these impressions clearly show the original dental pattern of the genus to have been identical to the basic dentition of the Lucinacea (Plate 28, figs. 1–8). As in recent lucinoids, *Babinka* has a large, lobed tooth in the right valve which fits between two smaller teeth in the left valve.

The ligament in the Lucinacea is opisthodetic; the principal ligament elements normally occupy an obscure groove in the hinge plate posterior to the cardinal dentition. In addition, the dorsal-hinge region posterior to the umbones normally shows a slight gape where elements of the ligament were exposed on the surface. Anterior to the umbones, recent lucinoids commonly show a well-developed lunule. The hinge region and ligament attachment area in *Babinka* show this same pattern. As in recent lucinoids, *Babinka* has a faint ligament groove and ligament gape posterior to the cardinal dentition, and the genus also shows the characteristic anterior lunule (Pl. 27, figs. 1, 2). In all features of the hinge and ligament, *Babinka* is a typical lucinoid bivalve.

LIFE HABITS

Silurian and younger fossil lucinoid bivalves almost certainly shared the adaptations for deeply buried suspension feeding seen in all recent Lucinacea (Allen, 1958) because the fossils show characteristic morphologic features, such as the elongate anterior adductor scar, which are directly related to that mode of life. Although the evidence is less conclusive for *Babinka*, it seems likely that it had similar habits.

The strong multiple pedal attachment muscles in *Babinka* suggest a large active foot which had probably only begun to develop the extremely extensible, cylindrical form of later Lucinacea. If this were the case, then *Babinka* would have been a rather shallow burrower, for the depth of burial in the Lucinacea is controlled by the degree of extensibility of the foot. *Babinka* may not have had the ability to form a distinct, mucous-

lined inhalent tube, but instead might have merely used repeated extrusions of the foot to maintain a crude anterior opening to the surface through a relatively thin cover of overlying sediment (text-fig. 6). Such habits would be a likely early stage in the development of the typical lucinoid anterior inhalent tube.

As discussed earlier, the 'elongate impression' below the anterior adductor in *Babinka* may represent a specialized area of the mantle which functioned as a preliminary ciliary sorting area for food particles brought in by the anterior inhalent current. A specialized sorting area on the mantle below the adductor is a likely preliminary step in the adaptive
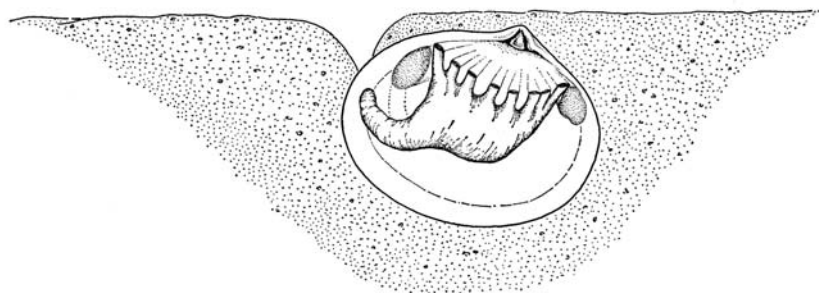
TEXT-FIG. 6. Inferred life position of *Babinka*. Compare with text-fig. 4.

trend leading to dorsal extension of the adductor muscle in the same position. The gills of *Babinka* were probably already functioning as food-gathering organs which filtered particles directly from the incoming water, and which also received food from ciliary tracts on the surface of the mantle and visceral mass.

In summary, *Babinka* probably was a buried suspension feeder which lived just below the surface of the sediment, drawing in nutrient-laden water through an anterior depression in the sediment surface maintained by extrusion of the foot. The foot was probably strong and active, enabling the animal to burrow and move through the substrate with ease. The animal probably fed by ciliary trapping and sorting of small food particles on the surface of the mantle, visceral mass, and gills.

SYSTEMATIC DESCRIPTIONS

GENUS BABINKA BARRANDE 1881

Type species, by monotypy and subsequent designation of Růžička and Prantl 1960 (*p.* 48), *Babinka prima* Barrande 1881, pl. 266, figs. VI, 1–16.

Discussion. The genus is known only from the type species found in the lowest Middle Ordovician of the Bohemian Basin, Czechoslovakia. The alternative generic name *Anuscula* was simultaneously proposed by Barrande and should be treated as a junior objective synonym of *Babinka*. The name *Babinka* is undoubtedly valid because no additional generic or specific names have been proposed for the type species, and there are no other named species which are likely to be subjectively synonymous with *Babinka prima*.

Babinka prima Barrande

Plate 26, figs. 3–12; Plate 27, figs. 3–5; Plate 28, figs. 1–4, 9–14

Babinka prima Barrande, 1881, pl. 266, figs. vi, 1–16. Vokes, 1954, p. 234, fig. 1. Cox, 1959,
p. 204, fig. 2. Růžička and Prantl, 1960, p. 48. Horný, 1960, p. 480, pl. 1, figs. 1, 2. Vogel,
1962, p. 235, pl. 5, figs. 5–6. [not?] Thoral, 1935, p. 162, pl. 13, figs. 4–5.

Revised description. Medium-sized, anteriorly extended, compressed, equivalved bivalves
showing considerable shape variability (probably exaggerated by post-depositional dis-
tortion in many specimens). Surface sculpture of fine, concentric ridges (Pl. 26, figs.
3–6). One articulated specimen preserving the original shell material shows prominent
lunule (Pl. 27, fig. 2). Dentition consisting of one large, triangular, cardinal tooth with

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EXPLANATION OF PLATE 26

All specimens of *Babinka prima* are from concretions from the Šárka Beds (Middle Ordovician) at
Osek, near Rokycany, Czechoslovakia.

Figs. 1, 2. *Codakia* (*Ctena*) *sp*. Recent, Bikini Island, ×1·5, showing characteristic anteriorly-extended
shape of the Lucinacea. 1, Right valve, YPM 23869. 2, Left valve, YPM 23868.

Figs. 3–6. *Babinka prima* Barrande. A series of latex casts of natural external moulds, showing the
shape and sculpture of the original valve exteriors. 3, Left valve, YPM 23858, ×2 (see also Pl. 28,
fig. 13). 4, Right valve, NMP ČD228a (cast shown in photograph deposited in YPM), ×1·5. 5, Left
valve, NMP ČD228b (cast shown in photograph deposited in YPM), ×1·5. 6, Left valve, unnumbered
NMP paratype (cast shown in photograph deposited in YPM), originally figured by Barrande, 1881,
as fig. vi, 16 of plate 226, ×1·5 (see also fig. 11 below).

Figs. 7–12. *Babinka prima* Barrande. A series of internal moulds of right valves (7–9) and left valves
(10–12), ×2. 7, Unnumbered MCZ specimen (see also Pl. 28, fig. 12). 8, Unnumbered NMP para-
type, originally figured by Barrande, 1881, as figs. vi, 10–12 of plate 266. 9, Unnumbered NMP
paratype, originally figured by Barrande, 1881, as figs. vi, 13–15 of plate 266. 10, Lectotype, NMP
ČD229a, originally figured by Barrande, 1881, as figs. vi, 7–9 of plate 266, and refigured by Horný,
1960, as fig. 2 of plate 1. 11, Unnumbered NMP paratype, the external mould of this specimen was
originally figured by Barrande, 1881, as fig. vi, 16 of plate 266 and is reillustrated here as fig. 6
above. 12, Paratype, NMP ČD229b, originally figured by Barrande, 1881, as figs. vi, 4–6 of plate 266.

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
NMP = Národni muzeum v Praze, Prague, Czechoslovakia. YPM = Peabody Museum of Natural
History, Yale University, New Haven, Connecticut, U.S.A.

EXPLANATION OF PLATE 27

All specimens of *Babinka prima* are from concretions from the Šárka Beds (Middle Ordovician) at
Osek, near Rokycany, Czechoslovakia. Abbreviations as on explanation of Plate 26.

Fig. 1. *Codakia orbicularis* (Linne). Recent, Barbados, West Indies, YPM 23865, dorsal view showing
posterior ligament gape (dark area to left of umbones) and lunule (to right of umbones), ×2.

Figs. 2–5. *Babinka prima* Barrande. 2, Dorsal view of unnumbered NMP specimen preserving original
shell material, showing posterior ligament gape (dark area to left of umbones; internal matrix
darkened on photograph for contrast) and lunule (to right of umbones), ×3. 3, Right view of
specimen shown in fig. 2, ×3. 4, Unnumbered NMP specimen, a well-preserved internal mould of
a left valve (photo. by Prof. N. D. Newell), ×4. This specimen was figured by Horný, 1960, as fig. 1
of plate 1. 5, Unnumbered NMP specimen, a well-preserved internal mould of a right valve showing
the complete pattern of muscle impressions, ×3. Other photographs of this specimen are included
on Plate 28 (figs. 4, 9–11).

Figs. 6, 7. *Ilionia prisca* (Hisinger). Silurian, Gotland, Sweden. 6, YPM 23870, right view of articulated
internal mould showing general shape and elongate anterior adductor muscle scar, ×1. 7, YPM
23871, left view of articulated internal mould showing general shape and adductor muscle scars, ×1.

raised median ridge in right valve, two smaller wedge-shaped cardinal teeth in left valve; lateral surfaces of teeth covered with fine, widely spaced parallel ridges (Pl. 28, figs. 1–4). Short, weak ligament groove along dorsal margin posterior to cardinal teeth (Pl. 28, figs. 1–4); slight ligamental gape along dorsal margin behind umbones (Pl. 27, fig. 2). Prominent anterior and posterior adductor muscle scars; posterior scar strongest in rounded area at ventral extremity, anterior scar strongest in elongate-oval area at ventral extremity (Pl. 28, figs. 9, 10, 12, 14). Faint, elongate, crescent-shaped depression ('elongate impression') extending ventrally from anterior adductor scar (Pl. 28, figs. 10, 11; text-fig. 1). Irregularly rounded pedal muscle scars adjoin dorsal side of adductor scars. Six additional pairs of pedal muscle scars between the adductors, becoming much stronger in rounded area at ventral extremity (Pl. 28, figs. 9, 10; text-fig. 1). Adductor and some pedal scars show faint concentric growth increments parallel to the advancing margin (Pl. 28, figs. 9, 10). Five posterior pairs of six central pedal scars bounded ventrally by about twenty-five smaller and more closely spaced, rounded muscle scars which probably represent the site of gill attachment (Pl. 28, figs. 9–11; text-fig. 1). Pallial line non-sinuate (Pl. 28, fig. 14). Original shell material preserved on a single articulated specimen showing fine, radial structural elements (Pl. 27, fig. 3); shell material and structure otherwise unknown.

Types. Lectotype, by designation of Růžička and Prantl (1960, p. 48), the left valve shown by Barrande, 1881, as figures VI, 7–9 of plate 266; No. ČD 229a in the Barrandeum collections of the Národni muzeum v Praze [National Museum], Prague, Czechoslovakia. Type locality: Vosek [= Wosek, Osek], Czechoslovakia. Stratigraphic position: d_1 [Šarka beds], Middle Ordovician [approximately Llanvirn]. Paratypes: one left valve and two right valves glued to the same plaque and bearing the same number as the lectotype, and two additional unnumbered right valves and one unnumbered left valve in the same collection. These seven specimens were figured by Barrande, 1881, as figures VI, 1–6 and 10–16 of plate 266. All were collected at the same horizon and locality as the lectotype.

Material. This revised description was based on personal examination of about 100 specimens. These include the lectotype, paratypes, and about ninety additional specimens in the following collections: Národni Muzeum, Prague, Czechoslovakia (about eighty specimens); Yale University Peabody Museum, New Haven, Connecticut, U.S.A. (six specimens); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. (one specimen). Dr. Radvan Horný of Prague informs me that the siliceous concretions in which *Babinka* occurs can rarely be collected today from the Šárka beds. The 100 studied specimens represent the bulk of the previously collected examples of *B. prima*, and it is unlikely that the species will ever be known from many additional Bohemian specimens.

Occurrence and preservation. The species is known with certainty only from the Šárka beds (approximately Llanvirn or lowest Middle Ordovician, see Horný, 1963) in the vicinity of Prague, Czechoslovakia. An occurrence of the species in Lower Ordovician rocks of southern France has also been reported (Thoral, 1935), but the illustrated specimens in Thoral's report cannot be positively recognized as *B. prima*, and the occurrence will require additional study before it can be accepted without question.

In addition to *Babinka*, the fauna of the Šárka beds includes the bivalve genera '*Leda*', '*Nucula*', and *Redonia*, as well as species of monoplacophorans, gastropods, hyolithids, ostracods, and trilobites (Barrande, 1881; Horný, 1963). The fauna occurs in small, dark, rounded, siliceous concretions which must be broken open to reveal the fossils. Most specimens in these concretions are preserved as sharp internal and external moulds separated by a space representing the site of the original shell material. All the examined specimens of *Babinka* are preserved in this way except for a single articulated specimen which preserves somewhat abraded and recrystallized original shell material (Pl. 27, figs. 2, 3). In most specimens of *Babinka* the concave external mould was discarded when the concretions were originally broken, and only the convex internal moulds, showing impressions of the internal shell features, are found in the collections. Fortunately, a few of the external moulds were not discarded, and latex casts of these provide additional knowledge of the external shape and sculpture of the valves. Most specimens of *Babinka* are disarticulated but otherwise well-preserved single valves; right and left valves occur in about equal abundance. Approximately 10 per cent. of the specimens preserve both valves in close articulation.

CONCLUSIONS

1. A reconsideration of the complex muscle-scar pattern of the problematic Middle Ordovician bivalve *Babinka* (Barrande, 1881) indicates that the adductor and pallial muscles of the genus were similar to those found in most other isomyarian bivalves.

EXPLANATION OF PLATE 28

All specimens of *Babinka prima* are from concretions from the Šárka Beds (Middle Ordovician) at Osek, near Rokycany, Czechoslovakia. Abbreviations as on explanation of Plate 26.

Figs. 1–4. *Babinka prima* Barrande. A series of latex casts of the hinge regions of internal moulds, showing the nature of the original dentition. 1, Left valve, YPM 23862, ×5. 2, Right valve, YPM 23861, ×5. 3, Left valve, paratype NMP ČD229b (cast shown in photograph deposited in YPM; sockets darkened on photograph for contrast; see also Plate 26, fig. 12), ×5. 4, Right valve, unnumbered NMP specimen (cast shown in photograph deposited in YPM). Other photographs of the same specimen are figs. 9–11 of this plate, and fig. 5 of Plate 27.

Figs. 5, 6. *Diplodonta punctata* Say. Recent, Kingston Harbour, Jamaica, dentition, ×8, showing similarity in tooth pattern between *Babinka* and the lucinoid Family Diplodontidae. 5, Left valve, YPM 23863. 6, Right valve, YPM 23864.

Figs. 7, 8. *Divaricella sp.* Recent, New Zealand, dentition, ×4, showing similarity in tooth pattern between *Babinka* and the cardinal dentition of the Family Lucinidae. 7, Left valve, YPM 23866. 8, Right valve, YPM 23867.

Figs. 9–14. *Babinka prima* Barrande. 9–11, Three views of unnumbered NMP internal mould of a right valve showing the complete pattern of muscle-scar impressions. Other photographs of this same specimen are fig. 4 of this plate and fig. 5 of Plate 27. Fig. 9 shows the posterior adductor-pedal scar and the central pedal and gill scars, ×5. Fig. 10 repeats the central scars and shows the anterior adductor-pedal scar and 'elongate impression', ×5. Fig. 11 is an enlargement of the fourth pedal scar and associated gill scars, ×10. 12, Unnumbered MCZ specimen, ×5, internal mould of right valve showing anterior adductor muscle scar and 'elongate impression' (see also Pl. 26, fig. 7). 13, YPM 23858, latex cast of dorsal region of articulated internal mould, showing nature of dental articulation as viewed from the interior side of closed valves. The base of the single large right valve tooth projects downward between the two smaller teeth of the left valve, ×5 (a cast of the external mould of this specimen is shown in fig. 3 of Pl. 26). 14, Unnumbered NMP internal mould of left valve, showing posterior pedal muscle scars, posterior-adductor pedal muscle scar, and non-sinuate posterior pallial line, ×3.

Babinka differs from other bivalves in having eight well-developed pairs of regularly spaced pedal muscles above and between the adductors instead of the more usual pattern of two to five pedal muscle pairs. In addition, *Babinka* shows a unique linear series of much smaller scars below some of the pedal muscle pairs. These scars probably mark the site of gill muscle attachment.

2. The multiple pedal and gill musculature of *Babinka* may reasonably be considered to represent an inheritance from some monoplacophora-like ancestor as has been repeatedly suggested, for the pattern of these muscles is almost identical to that found in recent *Neopilina* and some early fossil Monoplacophora. In all morphologic features other than the pedal and gill muscles, *Babinka* is a typical isomyarian bivalve.

3. Both stratigraphically and morphologically, *Babinka* is an ideal ancestral form for the first lucinoid bivalves which appear abruptly in Middle Silurian deposits. Morphological features of *Babinka* which are strongly suggestive of lucinoid affinities are: (1) the characteristic anteriorly expanded shell shape, (2) the elongate anterior adductor muscle and associated 'elongate impression', (3) the simple, non-sinuate pallial line, and (4) the typical lucinoid hinge, dentition, and ligament. *Babinka* differs from other lucinoid bivalves only in the pattern of pedal and gill muscle scars.

4. Recent lucinoid bivalves all share adaptations for life as deeply buried suspension feeders receiving nutrient-laden water into the mantle cavity through a unique, mucous-lined, anterior inhalent tube constructed by the foot. The morphology of *Babinka* suggests that it was also an infaunal suspension feeder with an anterior inhalent current. The large foot probably served not only for locomotion and digging, but also to maintain an anterior inhalent opening to the surface of the sediment.

5. *Babinka* is one of the first bivalves to appear in the fossil record. The genus probably represents a transitional evolutionary link between the successful Silurian to recent bivalve Superfamily Lucinacea and some monoplacophora-like molluscan ancestor (text-fig. 5). The transitional evolutionary position of *Babinka* indicates that lucinoid bivalves arose independently from a non-bivalved ancestor, and raises fundamental questions regarding the evolutionary history and classification of the Bivalvia. These more general topics will be the subject of a separate paper (McAlester, 1965).

Note added in proof. After the section above on 'Occurrence and preservation' was prepared, I have had an opportunity to visit the University of Montpellier, France, where Professor J. Avias kindly made available the specimens from southern France described as *Babinka prima* by Thoral (1935). Thoral's collections contain about three dozen small internal moulds which are almost certainly conspecific with the Bohemian specimens of *B. prima*. The specimens are all poorly preserved and contribute no new morphologic information, but they do extend both the geographic and stratigraphic range of the species. Most of Thoral's material was collected in the 'neighbourhood of St. Chinian' (Montagne Noire region) from rocks which he considered to be of upper Tremadoc age. These specimens may therefore be slightly older than the Bohemian occurrence of *B. prima*.
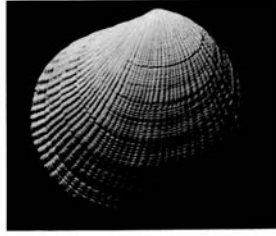
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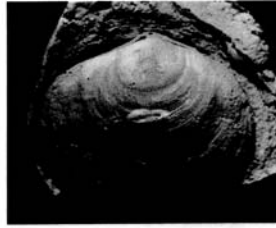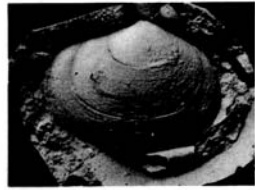Yale University,
New Haven,
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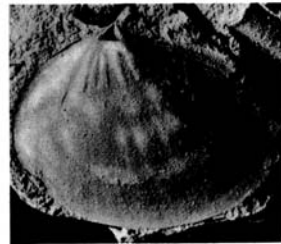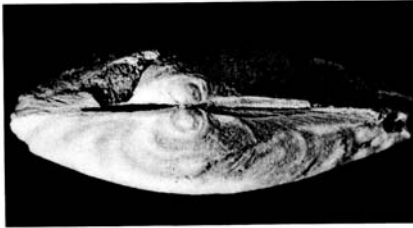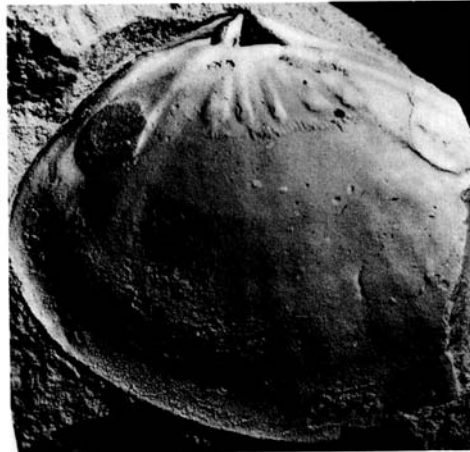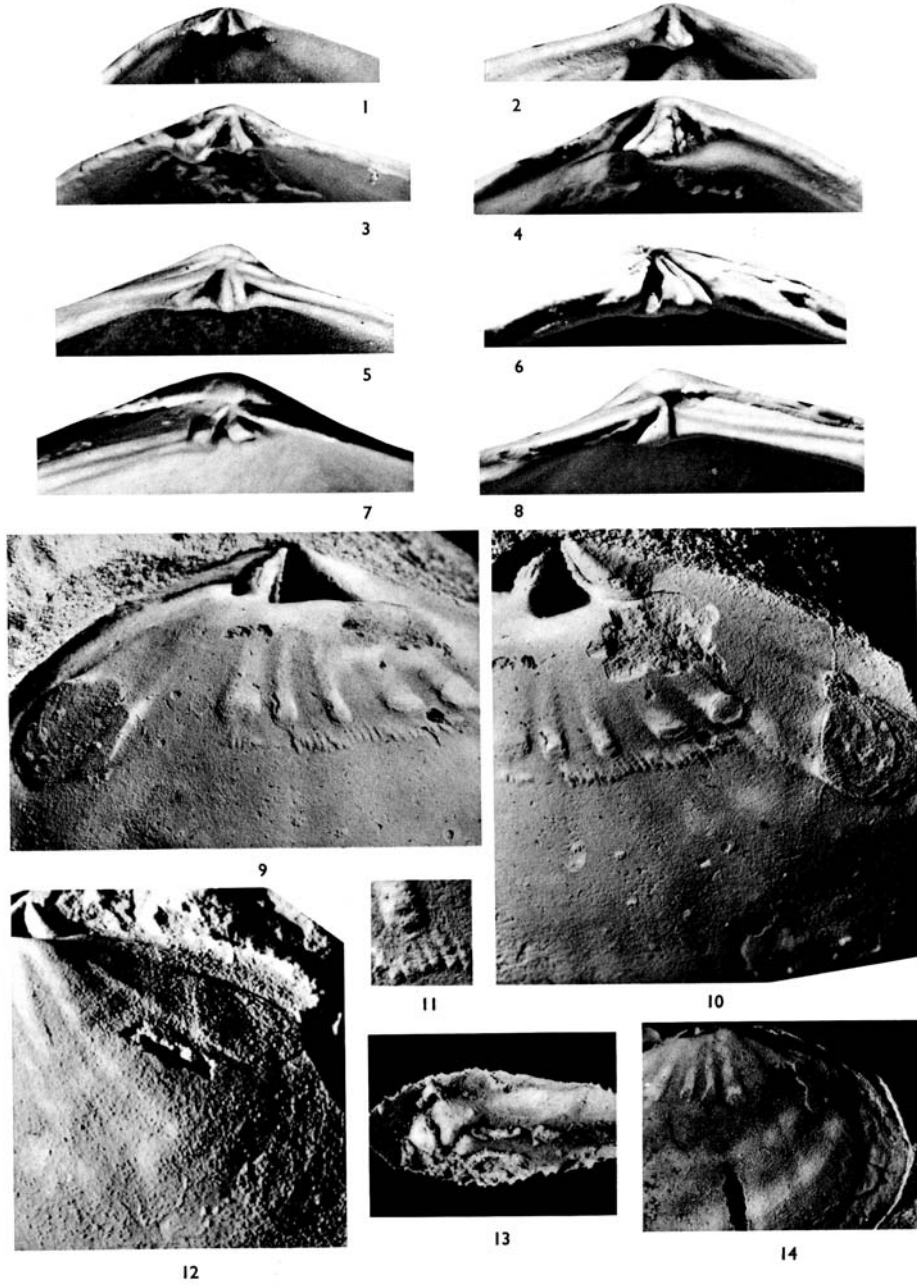McALESTER, Ordovician lucinoid *Babinka*

McALESTER, Ordovician lucinoid *Babinka*

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