Larval development and relationships of *Mimospira* – a presumably hyperstrophic Ordovician gastropod

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The embryonic shell of *Mimospira* is smooth, conical in shape with a slight sinistral twist, approximately 0.4 mm in diameter. A significant increase in mortality at the end of the embryonic stage of shell development and a lack of any other juvenile mortality peaks indicate the occurrence of metamorphosis at the beginning of mantle development. The columella and internal whorls developed closely to the end of the embryonic stage or earlier. Features of coiling show high population variability. Larval development of *Mimospira* is quite unlike that of euomphalid gastropods, which are currently classified in the same suborder, Macluritina. Euomphalids have coiled, slightly orthostrophic or isostrophic embryonic shells. The origin of hyperstrophy in *Maclurites* in the orthostrophy of *Ceratopea–Orospira*-like forms is suggested. Evolutionarily original hyperstrophy (here termed antistrophy) is thus restricted to the families Clisospiridae and Onychochilidae. A new suborder, Mimospirina, is proposed for them. □ *Monoplacophora, Gastropoda, new suborder, Mimospirina, Clisospiridae, Onychochilidae,* Mimospira, *larval development, evolution, torsion, Ordovician, Sweden, Poland, N5049 N5824 E1351 E2038.*

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An Early Ordovician genus, *Mimospira,* and related high-spired sinistral gastropods grouped in the families Onychochilidae and Clisospiridae, has been treated as a member of an early branch of originally hyperstrophic gastropods, the Macluritina. According to Knight et al. (1960) the Macluritina arose from the Bellerophontina (treated by them as isostrophic Gastropoda showing torsion) as an independent group distinct from other early gastropods. The Macluritina are suggested to possess paired ctenidia and other organs but the occurrence of hyperstrophy is inferred from the position of the channel, presumed to be exhalant, occupying a ridge close to the umbilicus (Knight 1952). The most important argument supporting hyperstrophy of *Maclurites* is the direction of coiling of its calcified operculum (Knight 1952). No operculum of any other representative of the Macluritina is yet known. Study of the larval development of the shell thus appears to be an important tool for recognizing both the direction of shell coiling and the relationships of this group.

Methods of inference

The morphology of the gastropod shell, like that of shells of other animals produced by marginal accretion, contains much information on the ontogenetic development of the animal. Methods of reading of this 'inscription' have been developed by many students of Recent gastropods (for a review see Jablonski & Lutz 1980). The key points of the majority of studies are the possibilities of distinguishing shells of planktotrophic from lecithotrophic larvae and/or embryonic stages developing within the egg capsule from free-living larval stages and from creeping post-larval stages. Numerous Recent gastropods show (1) a smooth initial shell corresponding to embryonic stage of development within the egg capsule; (2) an ornament of growth lines in the shell of the free-living veliger stage; and (3) an abrupt change in shell morphology indicating metamorphosis, i.e. the beginning of an adult, crawling mode of life (see i.a. Robertson 1971; Jung 1975; Bouchet 1976). In the first detailed study of Early Palaeozoic molluscan larvae (Dzik 1978, 1980) this correlation between changes in shell ornamentation and developmental events has been assumed, primarily because Recent pteropods, the closest analogues of Palaeozoic hyoliths and tentaculites, develop in such a way (Lalli & Conover 1976). However, application of this method of inference to early gastropods and monoplacophorans appears disputable (Dzik 1981). In the development of many Recent gastropods the em-

Fig. 1. Internal mold of a juvenile shell of *Mimospira* sp., Arenigian (Kundan) from the Gullhögen quarry, sample G-8, Skövde, Sweden; × 100.

bryonic shell is not confined to the stage of development within the egg capsule (Robertson et al. 1970; Iwata 1980), the ornamented larval shell is not restricted to the free-living veliger stage (Hadfield et al. 1972; Soliman 1977), and the stable indication of arrested growth does not necessarily correspond to any metamorphosis (Robertson et al. 1970; Robertson 1970). It appears then that the only fully substantiated inference on developmental stages of extinct molluscs may concern the time of development of the mantle (boundary between embryonic and larval shells) and metamorphosis (strong change of larval ornamentation or loss of larval apertural modifications). It has also been suggested (Dzik 1978, 1981) that a very sharp peak in distribution of mortality may indicate metamorphosis.

In this paper, to avoid misunderstanding, I use the terms embryonic shell or stage to identify the stage of active function of the shell gland (it should rather be named shell-gland conch or stage), and larval shell or stage for the stage in which the mantle functions prior to metamorphosis, whether the gastropod is free-living, whether it develops within an egg capsule or has a lecithotrophic or planktotrophic veliger.

Larval development of *Mimospira*

Sinistrally coiled juvenile shells of *Mimospira* are very common in acid-insoluble residues of Early Ordovician limestones from the Baltic area and the Holy Cross Mts., Poland, in some samples dominating assemblages of larval molluscan shells. Some beds contain hundreds of *Mimospira* shells per kilogram. Adult shells are much less common, except at some unusually fossiliferous localities (see Wängberg-Eriksson 1979). The usual mode of preservation is as an internal mold impregnated with chamosite or hematite (Fig. 1). Preserved impressions of the apertural margin with basal lip (Fig. 2) indicate that these are not infillings of apices of adult shells but real juveniles. Common negative molds allow study also of external shell morphology, but natural casts, with the shell impregnated with chamosite (?) (Fig. 3), are the best type of preservation. Details of growth-line distribution can be studied under the SEM in the latter cases.

Fossil assemblages of internal molds of *Mimospira* shells show a peak in size-frequency distribution at a shell diameter of slightly more than 0.4 mm (Fig. 2). This size of internal mold (Fig. 3B) corresponds to a remarkable change in external morphology, which is well shown on natural casts of shells (Fig. 3A, C, E). This change, not notable on internal molds, concerns both the shape of the shell and its surface ornamentation. Shells less than 0.4 mm in diameter are almost conical, with an oval apex; growth lines, if they occur, are very indistinct and probably appeared close to the end of this stage. It therefore seems to be an embryonic shell, produced by the entire surface of the shell gland. Change in ornamentation can hardly be interpreted as effected only by gradual development of the mantle. The peak in mortality rather suggests the presence of more profound developmental events at that moment, such as hatching or metamorphosis. Because mortality gradually decreases after development of the mantle (Fig. 2), with no other significant peak, it seems quite possible that metamorphosis really occurred at that time, but it does not rule out hatching at the same moment. Development of *Mimospira* seems to be similar to that of the associated pleurotomariid, *Clathrospira* (see Dzik 1978: Fig. 5A), although shapes of their embryonic shells are not similar.

Juvenile shells of *Mimospira* show considerable variability in all samples studied, especially with respect to the number of whorls. Some specimens have twice as many whorls as others of the same size (Fig. 2). Similar variability shown by internal molds of Cambrian gastropods was a reason for denying their gastropod affinities (Yochelson 1975). It must be noted that other Ordovician gastropod species are usually not so vari-

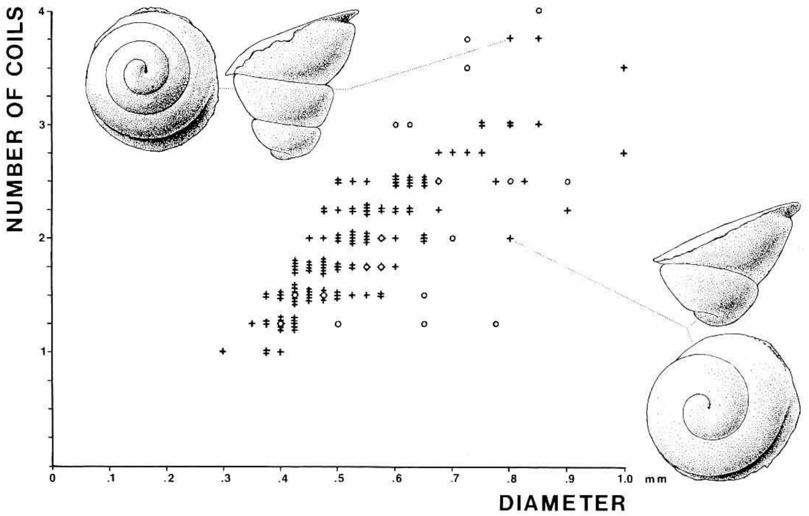


Fig. 2. Diameter of juvenile shells of *Mimospira* sp. plotted against number of whorls; only specimens with preserved apertures have been measured; circles – erratic boulder E-145 of the Folkeslunda Limestone, Llanvirnian (Lasnamägian), Mochty near Zakroczym, Poland; crosses – sample G-1 of the Vikarby Limestone, Llanvirnian (Lasnamägian), Gullhögen quarry, Skövde, Sweden. Drawings of extreme morphotypes added.

able. 'Worms' described by Bockelie & Yochelson (1979) from the Ordovician of Spitsbergen probably represent many unrelated gastropod and monoplacophoran species. The question arises whether this variability of internal molds represents a real larval variability or if it indicates variability in later deposition of an apical callus inside the shell. The presence of a clearly visible aperture in most specimens indicates without doubt that the columella and first whorls were produced no later than just after development of the mantle in the embryo (or larva). The variability discussed must therefore express at least high variability in the internal shell morphology of newly settled postlarval animals.

Even if such a wide larval variability of *Mimospira* is accepted it would not be an unusual case among Gastropoda. Larval shells of Recent vermetids (Hadfield et al. 1972) vary in size and shape due to the nurse yolk that must be ingested by developing embryos. Also the developmental pattern, direct or indirect (with free-living veliger or not) is variable and seems to be correlated more with the amount of nurse yolk available to each embryo than with egg size (Hadfield et al. 1972, p. 98). Some Recent architectonicid populations show a bimodal size-frequency distribution of larval shells (Robertson 1970, p. 80). Significant variability in size has also been noted in Recent pteropods (Spoel 1975). Veliger shells of abnormal shape are not uncommon among gastropods (Soliman 1977).

Evolutionary relationships of *Mimospira*

Currently the families Clisospiridae Miller, 1889 Onychochilidae Koken, 1925, both including genera closely related to *Mimospira,* are assigned to the suborder Macluritina, which groups these families with the Macluritidae and Euomphalidae (Knight et al. 1960; Horný 1965; Wängberg-Eriksson 1979). The Macluritina is thought to comprise hyperstrophic derivatives of the Bellerophontina (Knight et al. 1960). Hyperstrophy is descriptive of falsely sinistral shell of animals that are otherwise dextral anatomically, with genitalia and excurrent siphon on the right (Knight 1952). Knight (1952) discussed and rejected the possibility that *Maclurites* is a sinistral gastropod on the basis of presence of an incision,

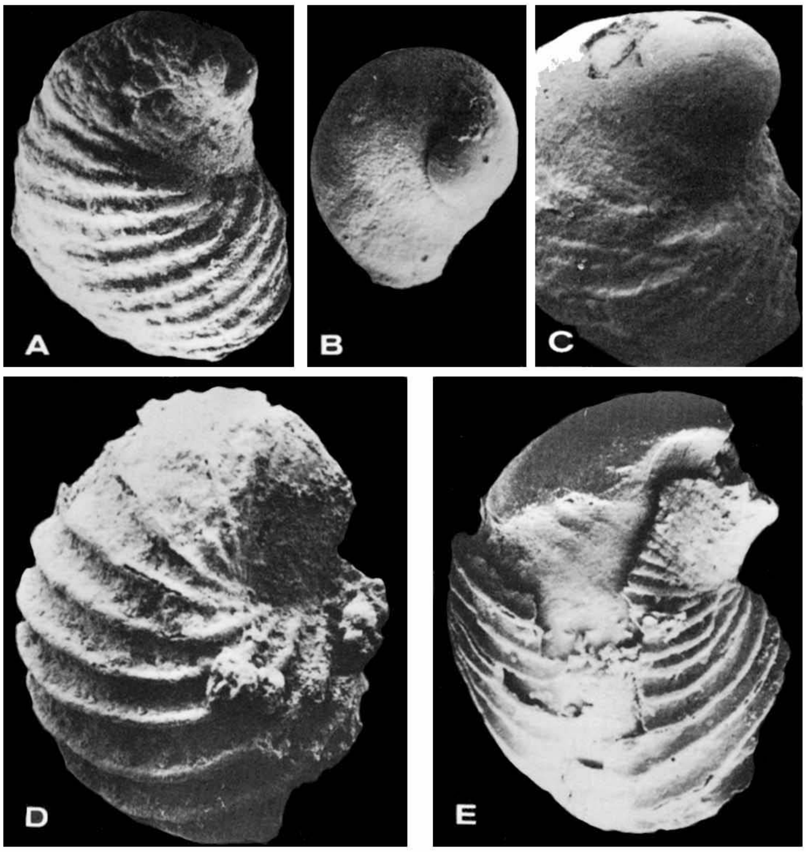


Fig. 3. Juvenile shells of *Mimospira* spp. from the Mójcza Limestone, Mójcza near Kielce, Poland. All × 100. □ A. Natural cast (original shell matrix impregnated with chamosite), ZPAL Gal/32, sample A-15, Llanvirnian (Aserian). □ B. Internal mold of embryonic shell, ZPAL Gal/33, sample A-10, Llanvirnian (Lasnamagian). □ C. Natural cast of juvenile shell, ZPAL Gal/34, sample A-29, Llanvirnian (Kundan). □ D. ZPAL Gal/35, sample A-4, Late Caradocian (? Jõhvian). □ E. ZPAL Gal/36, sample A-20, Early Caradocian (Kukrusean).

interpreted by him as anal, on the right side of the shell and because of the direction of coiling of the calcified operculum. But what could be the reason for development of dextral anatomy in its isostrophic bellerophontid ancestor? The only rational solution that I see to this antinomous problem is to consider *Maclurites* as a secondarily hyperstrophic derivative of dextral (orthostrophic) gastropods. Support for such an interpretation is given by the occurrence in the Early Ordovician, below the appearance of *Maclurites,* of dextrally coiled gastropods, from which the *Maclurites* shell could have been derived. These are the genera *Orospira* and *Ceratopea,* which possess low, widely umbilicate (phaneromphalous) shells and a massive, significantly calcified, operculum (Yochelson & Bridge 1957; Yochelson & Wise 1972). *Orospira* has been assigned to the Macluritina by Knight et al. (1960).

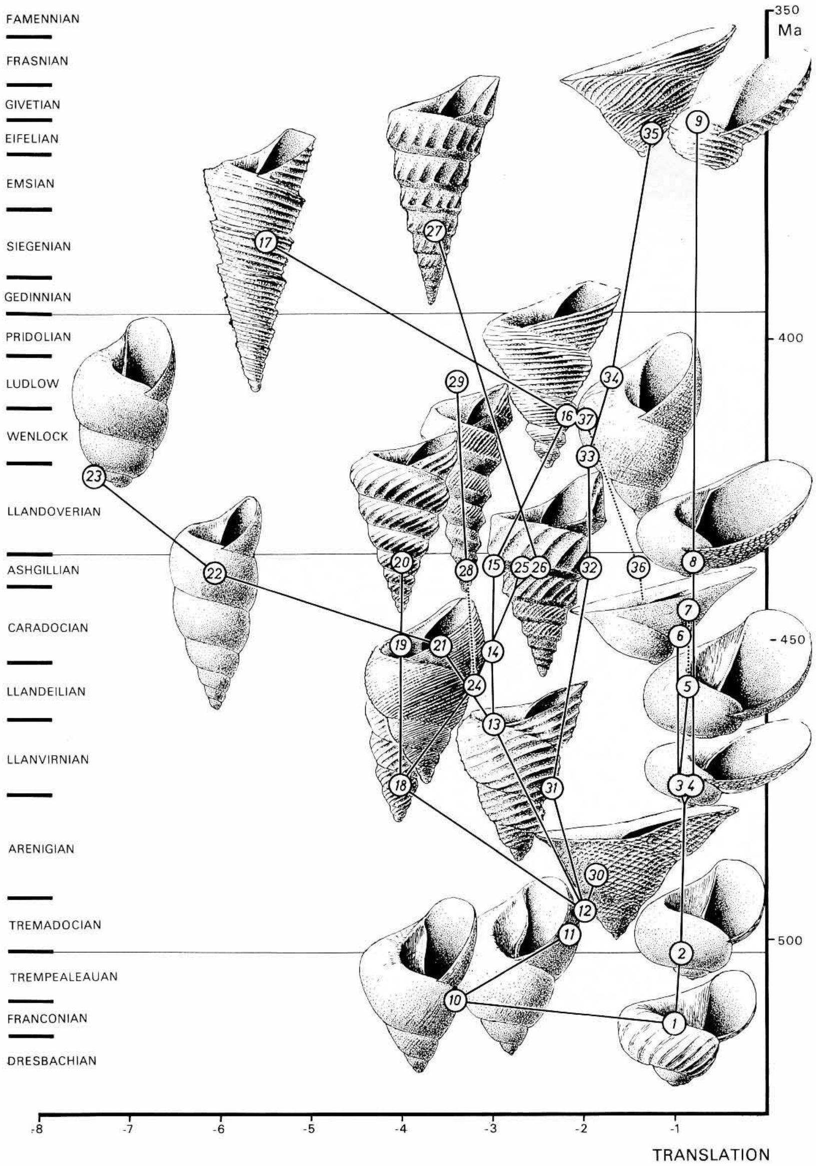
The widely phaneromphalous shell of *Orospira* has morphologic features that allow easy evolutionary development of hyperstrophy (Vermeij 1975). *Maclurites* can be derived from *Orospira* through *Helicotoma* and *Lecanospira* as intermediate shell morphotypes. This would mean that the Cambrian dextral gastropod *Schizopea* was probably the ancestor of *Maclurites* and that a long evolution of dextrality preceded development of hyperstrophy in *Maclurites*.

The theoretical derivation of *Maclurites* suggested above makes any relationship between *Maclurites* and the clisospirid–onychochilid stock improbable. Hyperstrophy seemingly developed in *Maclurites* later than the high, specialized shells of *Clisospira* appeared (Fig. 4). Strong support for this concept is provided by morphology of the embryonic shell of *Mimospira*, in which no indication of dextral coiling is seen. The *Mimospira* embryonic shell is rather high and sinistrally twisted, thus homeostrophic with the teleoconch. In this respect *Mimospira* is unlike Ordovician (Dzik 1978: Fig. 4C), Devonian, or Jurassic (Wendt 1968) representatives of the Euomphalidae, the closest relatives of *Maclurites*. All known euomphalid embryonic shells are planispiral or slightly orthostrophic, with one volution and an umbilical perforation. There are several reasons to believe that Recent Architectonicidae are euomphalid successors and consequently members of the suborder Macluritina. There is a rather complete fossil record that traces derivation of Recent *Architectonica* from Palaeozoic euomphalids. Along with the development of the characteristic low conical spire of *Architectonica* it is possible to trace changes in both shape and size of the embryonic shell. Ordovician euomphalids had embryonic shells about 0.2 mm in diameter (Dzik 1978); in the Early Jurassic they attained almost 0.3 mm, preserving the same shape (Wendt 1968). Late Cretaceous architectonicid species show a range in size diversity from 0.2 to 1.1 mm; in number of whorls from 1 to 2 1/4 respectively; and in shape from almost planispiral to slightly hyperstrophic ('first volution slightly submerged' – Sohl 1960, p. 66). Embryonic shells of Paleocene *Architectonica* are more hyperstrophic and larger (size from 0.6 to 0.8 mm; Amitrov 1978). Recent architectonicids possess significantly hyperstrophic embryonic shells as much as 1.7 mm in diameter (Robertson 1970). Development of hyperstrophy in the Architectonicidae was evidently a rather recent evolutionary innovation and has little bearing on their evolutionary relationships, despite conclusions based on purely neontological data (Robertson 1973).

It may be concluded that there is no reason to connect *Mimospira* and related forms with macluritid gastropods. Independently of having orthostrophic embryonic and hyperstrophic adult (*Maclurites* and *Palliseria*) or heterostrophic embryonic and orthostrophic adult shells (*Architectonica*) representatives of Macluritina were typically dextral gastropods. They, and *Mimospira* developed independently from a common isostrophic ancestor. Only the Clisospiridae and Onychochilidae appear to be direct successors of originally sinistral Cambrian gastropods (Fig. 4).

Soft anatomy and mode of life of *Mimospira*

The temporal distribution of shell characters suggests that clisospirids and onychochilids are derivatives of some Cambrian low-spired and phaneromphalous sinistral gastropods. *Kobayashiella circe* (Walcott) from the Late Cambrian of China seems to be closest to the supposed ancestor of the stock. Similar, low sinistral shells are widely known from the earliest Cambrian on but there are very few data regarding their external morphology. All are known from internal molds of juvenile or larval shells (Golubiev 1976; Missarzhevsky 1981). They could be interpreted, in the terms of Knight's (1952) and Knight et al.'s (1960) theory of the independent origin of dextral and originally sinistral gastropods, as close to the point of divergence in the development of anatomical asymmetry, indicating origin of the class. This involves the important question if clisospirids and onychochilids could be included in the class Gastropoda without destroying its monophyly. Torsion is the diagnostic feature of the class Gastropoda. It 'comprises displacement of the mantle-and-shell with the enclosed visceral mass moving in a counter-clockwise direction in the horizontal plane through an angle of 180 degrees in relation to the head and foot' (Yonge 1960, p. 12). Many opinions have been expressed regarding reasons for the evolutionary development of torsion in the early Gastropoda (i.a. Yonge 1960; Ghiselin 1966; Stanley 1979). It is obvious that a heavy shell carried by a moving animal tends to place its center of gravity in the back of the attachment of the soft body. In the case of spirally coiled (isostrophic) shells of bellerophontids only the presence of numerous muscle attachments around the shell aperture prevents rotation of the spire from an anterior to a posterior position (see Dzik 1981). Reduction of subanal and lateral muscle attachments, resulting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ASHGILLIAN
CARADOCIAN
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in the attachment of pedal muscles at only one point on the columella, allows the shell to be rotated in all directions (Peel 1980). In the case of an isostrophic shell, clockwise and counterclockwise directions of rotation (torsion) are equally preferable. Development of shell asymmetry significantly changes the position of the center of gravity, moving it laterally toward the apex of the spire. If an elevated spire would appear on the right side of an originally isostrophic shell that was oriented with its spire toward the head, clockwise torsion would be preferred. If the spire developed on the left side, counterclockwise torsion should have occurred. In the first case the shell is sinistral; in the second, dextral. Subsequent evolution that improved package of the internal organs would stabilize the direction of torsion even more.

It seems quite probable that Early Cambrian dextrally and sinistrally coiled, low-spired pelagiellids (i.a. see Golubiev 1976; Missarzhevsky 1981) represent initial stages of development of the two original modes of gastropod torsion. At the stage probably represented by pelagiellids, the direction of torsion probably had little adaptive importance as all internal organs were still symmetrical. It is even possible that sinistral and dextral shells belong to the same species of these ancient gastropods (Knight 1952, p. 43). If *Kobayashiella* and subsequently *Mimospira* are derivatives of sinistral Early Cambrian pelagiellids, there is little reason to suggest their dextral internal organization. Rather they had a sinistral internal anatomy, but of quite a different evolutionary origin than that of sinistral Recent gastropods. The term 'heterostrophy' in usual sense cannot be applied to the *Mimospira* shell for *Mimospira* did not have a dextral anatomy. I propose the term *antistrophy* to describe such primarily sinistral shells. Presentation of an antistrophic shell with the base upward, as applied also to hyperstrophic gastropods, still seems to be very reasonable.

Linsley (1977) proposed a mobile mode of life for *Onychochilus* and suggested that the shell spire projected over the head with the anus placed posteriorly in the basal incision. Reasons for reconstructing such an unusual position of the shell have not been quite clearly explained. As indicated above there is little probability that an incision near the base of *Matherella* and *Onychochilus* shells, which is probably homologous with the basal fringe of *Mimospira* and *Clisospira,* corresponds either to the exhalant sipho or to the basal incision of *Maclurites* shell. The exhalant sipho probably was placed at the periphery of the aperture, at the place that is transformed into an apertural angulation in *Antizyga* (cf. Fig. 4). The shell morphology of *Conoclisa*, *Clisospira*, and *Ferrogyra* is so similar to that of Recent *Calyptraea* (cf. Fig. 4) that a similar mode of life can be suggested for these animals. Recent Calyptraeidae are sessile filter-feeders (see Hoagland 1977), sensitive to suspended sediment (Johnson 1972). The same mode of life for *Clisospira* has previously been suggested by analogy with Recent xenophorids (Linsley et al. 1978). The small size of adults, however, may suggest analogy to

Fig. 4. Index of translation (see Raup 1966) estimated for better-known representatives of the suborder Mimospirina nov. plotted against time. Suggested relationships indicated by lines. Drawings of most characteristic forms added to show morphologic diversity. Not to scale. (1) *Kobayashiella circe* (Walcott), Chau-mi-tien limestone, Shantung. (2) *Scaevogyra sweezyi* Whitfield, Trempealeau Formation, Wisconsin. (3) *Laeogyra bohemica* Perner, Šárka Formation, Bohemia. (4) *Invertospira lamellifera* Horný, same. (5) *Helicotis rugifer* Koken, Folkeslunda (?) Limestone, Sweden. (6) *Versispira contraria* Perner, Letná Formation, Bohemia. (7) *Ferrogyra antiqua* (Perner), Vinice Formation, Bohemia. (8) *Pervertina gracilis* (Perner), Kosov Beds, Bohemia and Boda Limestone, Sweden. (9) *Hyperstrophema devonicans* Horný, Třebotov Limestone, Bohemia. (10) *Matherella saratogensis* (Miller), Hoyt limestone, New York. (11) *Matherellina walcotti* (Kobayashi), Wanwankou Dolomite, Manchuria. (12) *Mimospira helmhackeri* (Perner), Třenice Formation, Bohemia. (13) *Mimospira* sp., erratic boulder of Folkeslunda Limestone, Poland. (14) *M.* sp. indet. Wängberg-Eriksson, Kukruse Stage, Estonia. (15). *M. kallholniensis* Wängberg-Eriksson, Boda Limestone, Sweden. (16) *M. cochleata* (Lindström), Slite Beds, Gotland. (17) *Atracura candida* Horný, Řeporyje Limestone, Bohemia. (18) *Undospira?* sp. indet. Wängberg-Eriksson, *Gigas* Limestone, Sweden. (19) *Mimospira similis* Wängberg-Eriksson, Källa Limestone, Öland. (20) *Undospira turrita* (Koken), Red Jonstorp Formation, Sweden. (21) *Mimospira tenuistriata* Wängberg-Eriksson, Dalby Limestone, Sweden. (22) *Tapinogyra glaphyra* Wängberg-Eriksson, Boda Limestone, Sweden. (23) *Palaeopupa abrupta* Foerste, Brassfield Limestone, Ohio. (24) *Undospira striata* Wängberg-Eriksson, Furudal Limestone, Sweden. (25) *Bodospira kallholniensis* Wängberg-Eriksson, Boda Limestone, Sweden. (26) *B. undulata* Wängberg-Eriksson, same. (27) *Antizyga pagoda* Horný, Slivenec Limestone, Bohemia. (28) *Angulospira striata* Wängberg-Eriksson, Boda Limestone, Sweden. (29) *A.?* sp. indet. Wängberg-Eriksson, Hemse Beds, Gotland. (30) *Clisospira curiosa* Billings, Beekmantown Limestone, Quebec. (31) *C. ingrica* Koken, Kunda stage, Ingermanland. (32) *C. rugosa* Koken, Red Jonstorp Formation, Sweden. (33) *Conoclisa minuta* (Perner), Liteň Formation, Bohemia. (34) *C. schucherti* (Perner), Kopanina Formation, Bohemia. (35) *Antigyra indentata* (Perner), Koněprusy(?) Limestone, Bohemia. (36) *Laeogyra arvetensis* Wängberg-Eriksson, Boda Limestone, Sweden. Based mainly on data from Knight (1941), Horný (1964), and Wängberg-Eriksson (1979).

some Recent mobile opisthobranchs with a reduced shell. A shell shape very similar to that of *Mimospira* occurs also in the sedentary polychaete (?) *Anticalyptraea,* which is cemented to the substrate. Sinistrally coiled *Anticalyptraea,* with a wide apertural frill and anomphalous shells, occurs in the Silurian of Gotland and Bohemia (Horný 1965) and in the Late Silurian and the Middle Devonian of the Holy Cross Mts., Poland. Little is known about the early ontogeny and relationships of this peculiar fossil.

Taxonomic conclusions

If the presence of antistrophy in *Maclurites* is rejected, its presence in the Clisospiridae and Onychochilidae seems to be a sufficient reason for separating them from other archaeogastropods on at least the subordinal level. Several taxa of family or subfamily rank have been proposed for members of this group but, at the present stage of knowledge, it seems impossible to substantiate more detailed systematics than division into the two traditionally recognized families. I propose to diagnose them on the basis of umbilical and pseudoumbilical characters, which are seemingly unique among early gastropods.

Mimospirina new suborder

Diagnosis. – Asymmetry of the shell spire presumably opposite to that of other gastropods (antistrophic, i.e. originally sinistral). Soft anatomy probably with some signs of sinistrality but with paired main organs.

Onychochilidae Koken, 1925 (incl. Scaevogyrinae Wenz, 1938 emend. Knight et al. 1960; Hyperstropheminae Horný, 1964).

Emended diagnosis. – Basal angulation (but not a frill) delimits umbilicus, which does not exceed half of the shell diameter. Mainly low-spired and large forms; reticulate ornament common.

Genera included. – *Kobayashiella* Endo, 1937; *Scaevogyra* Whitfield, 1878; *Matherella* Walcott, 1912; *Matherellina* Kobayashi, 1937; *Invertospira* Horný, 1964; *Laeogyra* Perner, 1903; *Pervertina* Horný, 1964; *Versispira* Perner, 1903; *Hyperstrophema* Horný, 1964; *Onychochilus* Lindström, 1884; *Helicotis*? Koken, 1925.

Clisospiridae S. A. Miller, 1889 (incl. Trochoclisinae Horný, 1964; Atracurinae Horný, 1964).

Emended diagnosis. – Shell base with pseudoumbilicus, tending to be as wide as or wider than shell diameter, delimited by prominent rib or frill. Usually high-spired, minute shells ornamented by prominent growth lines.

Genera included. – *Mimospira* Koken, 1925 (incl. *Undospira* Wängberg–Eriksson, 1979); *Conoclisa* Horný, 1964 (incl. *Antigyra* Horný, 1964); *Clisospira* Billings, 1865; *Tapinogyra* Wängberg-Eriksson, 1979; *Antizyga* Horný, 1964 (incl. *Bodospira* Wängberg-Eriksson, 1979 and *Angulospira* Wängberg-Eriksson, 1979); *Atracura* Horný, 1964; ? *Ferrogyra* Horný, 1964; ? *Palaeopupa* Foerste, 1893.

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