

MORPHOLOGICAL VARIATION IN *HEMIGORDIUS HARLTONI* CUSHMAN & WATERS, 1928: REMARKS ON THE TAXONOMY OF CARBONIFEROUS AND PERMIAN HEMIGORDIOPSIDS

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Abstract. Nine morphotypes recognized within its population suggest that *Hemigordius harltoni* is a polytypic species. Narrowly discoidal to discoidal morphotypes are dominant in the population whereas lenticular ones are rare and sporadic. The degree of morphological variation in *H. harltoni* prompts us to question the validity of several previously named Carboniferous and Permian taxa. The definition of these taxa, generally based on few specimens, is far from being satisfactory to describe the intraspecific variability. Some named species are actually morphotypes belonging to highly variable species.

Riassunto. Il riconoscimento di nove morfotipi nelle popolazioni di *Hemigordius harltoni* suggerisce che si tratti di una specie politipica. I morfotipi da debolmente discoidali a totalmente discoidali sono dominanti nelle popolazioni, mentre quelli di forma lenticolare sono rari e sporadici. Il grado di variabilità morfologica in *H. harltoni* ci spinge a considerare la validità di diversi taxa definiti nel Carbonifero e nel Permiano. La definizione di questi taxa, generalmente basati su pochi esemplari, è lungi dall'essere soddisfacente per poter valutare la variabilità intraspecifica. Alcune delle specie nominali esistenti sono a nostro avviso morfotipi appartenenti a specie fortemente variabili.

Introduction

One of the frequently reported hemigordiopsid species from the Western Hemisphere is *Hemigordius harltoni* Cushman & Waters, 1928 (Cushman & Waters 1928 a, b, 1930; Galloway & Harlton 1930; Toomey 1972; Brenckle 1973; Brenckle et al. 1982; Groves 1983, 1984, 1986, 1992; Skipp et al. 1985; Altiner & Savini 1995; Mamet 1996). Particularly Groves (1984) made a clear description of the species, illustrating partially its morphological variation and emphasizing its biostratigraphic significance. His work demonstrated that *H. harltoni* is present not only in the Upper Pennsylvanian but also in the Lower

Pennsylvanian (Morrowan) rocks in the Midcontinent and western United States. In a more recent work, *H. harltoni* has also been reported from the Lower Pennsylvanian (Morrowan) of the Amazonas and Solimões basins, northern Brazil (Altiner & Savini 1995).

Based on several specimens obtained from boreholes in northern Brazil (Fig. 1), the morphologic variation of *H. harltoni* is known to occupy a much wider spectrum. This interpretation leads to the recognition of several morphotypes belonging to *H. harltoni*, each of which could be named as a different taxon according to the conventional approach in paleontology. Such an analysis questions arbitrary taxonomical limits and the validity of several previously introduced species in the Carboniferous and Permian, which could be morphotypes of highly variable species.

Morphologic variation in *Hemigordius harltoni*

In its type description, *H. harltoni* is defined as a species having a compressed test, circular in equatorial section with the early stages coiled in varying planes, the later ones becoming planispiral. The second tubular chamber is described as undivided and the middle portion of the test on either side is covered with a secondary growth of material largely concealing the sutures between adjacent whorls (Cushman & Waters 1928a).

Although this description is based on simple drawings of the type material from the Upper Pennsylvanian of Texas (USA), recent investigations revealed characteristic sections and parameters of this taxon. Groves (1984) described the species as a narrowly discoidal form with an irregular peripheral outline and coiling that is streptospi-

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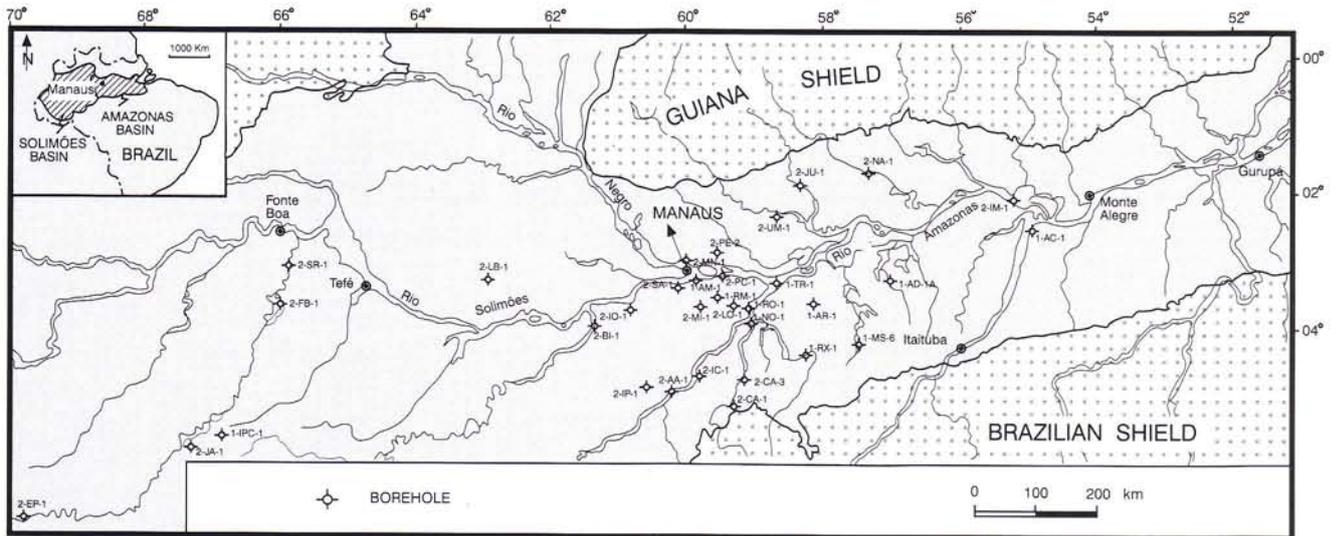


Fig. 1 - Distribution of boreholes which contain *Hemigordius harltoni* in the Amazonas and Solimões basins.

ral to sigmoidal and involute in the initial 2-3 volutions, then sigmoidal to nearly planispiral and evolve in the outer volutions. He added that side thickenings envelop the initial 2-4 volutions of typical specimens and are only rudimentary in other specimens. After giving other parameters of the taxon, he stated that *H. harltoni* differs from *H. simplex* by its early streptospiral to sigmoidal coiling and from *H. liratus* by its rounded periphery.

Based on several specimens obtained from the boreholes in northern Brazil (Fig. 1), the variation in the *H. harltoni* population is analysed in a much broader morphologic spectrum in this study. Forms vary from nearly planispiral to streptospiral, observed both in axial and equatorial sections (Pl. 1, fig. 1-35; Pl. 2, fig. 1-41; Pl. 3, fig. 10-14, 15 ?). Specimens illustrated in Pl. 3, fig. 1-9 do not belong to *H. harltoni* population. We have tentatively assigned them to *H. liratus* Cushman & Waters, 1928.

Within the population of *H. harltoni* 9 morphotypes have been distinguished (Fig. 2, a-i):

The **morphotype a** (Fig. 2) is characterized by narrowly discoidal tests (diameter: 210-560 μ ; width: 40-90 μ ; form ratio: 4.4-6.8) with 5 to 8 oscillating to planispiral whorls, outer ones being evolute. This morphotype has weakly developed lateral thickenings and a large proloculus (diameter: 40-60 μ).

Discoidal tests (diameter: 150-530 μ ; width: 60-

130 μ ; form ratio: 2.5-4.4) of the **morphotype b** (Fig. 2) consist of 5 to 6 oscillating whorls and a large proloculus (diameter: 35-75 μ). In diameter/width plots (Fig. 3), the discoidal morphotype b can be distinguished from the narrowly discoidal morphotype a by a different areal distribution. Lateral thickenings do not considerably increase in the morphotype a even if the diameter of the test increases in narrowly discoidal tests (Fig. 3). Discoidal forms of the morphotype b are characterized by tests with larger width.

The **morphotype c** (Fig. 2) is again a discoidal population (diameter: 290-510 μ ; width: 90-125 μ ; form ratio: 3.2-4.5) consisting of 7 to 8 whorls. The earlier 3 to 4 whorls are streptospirally coiled around a small proloculus (diameter: 10 μ). In diameter/width plots (Fig. 3), the morphotype c falls within the areal distribution of the morphotype b, however, the former differs from the latter by a small proloculus and streptospiral initial whorls.

Morphotypes d and e (Fig. 2) are characterized by lenticular tests. The basic difference is the presence of a large proloculus (diameter: 40-60 μ) and more aligned coiling in the morphotype d (diameter: 200-225 μ ; width: 95-105 μ ; form ratio: 2.0-2.4). Morphotype e (diameter: 130-300 μ ; width: 65-170 μ ; form ratio: 1.7-2.4), however, is characterized by a marked oscillation (streptospiral

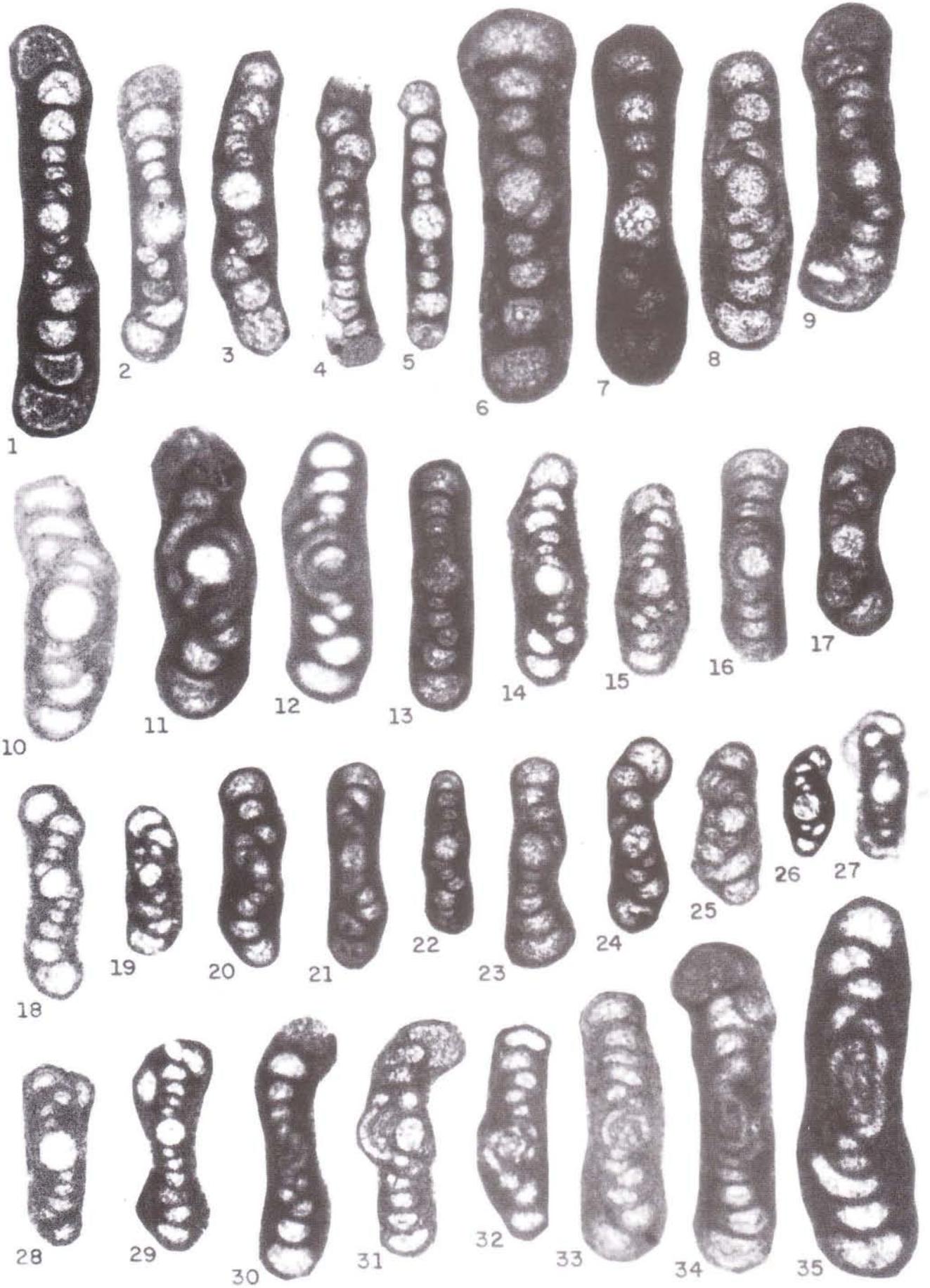
PLATE 1

All figures X 132

Fig. 1-35 - *Hemigordius harltoni* Cushman & Waters, 1928

1-5: Morphotype a; 6-16: Morphotype b; 17-26: Morphotype g; 27-29, 31: Morphotype h; 30, 32-35: Morphotype c.

1, 5, 22, 24: 1-AM-8-AM (Borehole location close to 1-AM-1-AM, Fig. 1), core 4; 2-4, 6-7, 9, 11, 13, 17, 20-21, 23, 25, 34: 2-CA-1-AM, core 7; 8, 18, 31-33: 1-AM-1-AM, core 14; 19, 29-30, 35: 1-AM-6A-AM (borehole location close to 1-AM-1-AM, Fig. 1), core 3; 26: 2-AA-1-AM, core 2.



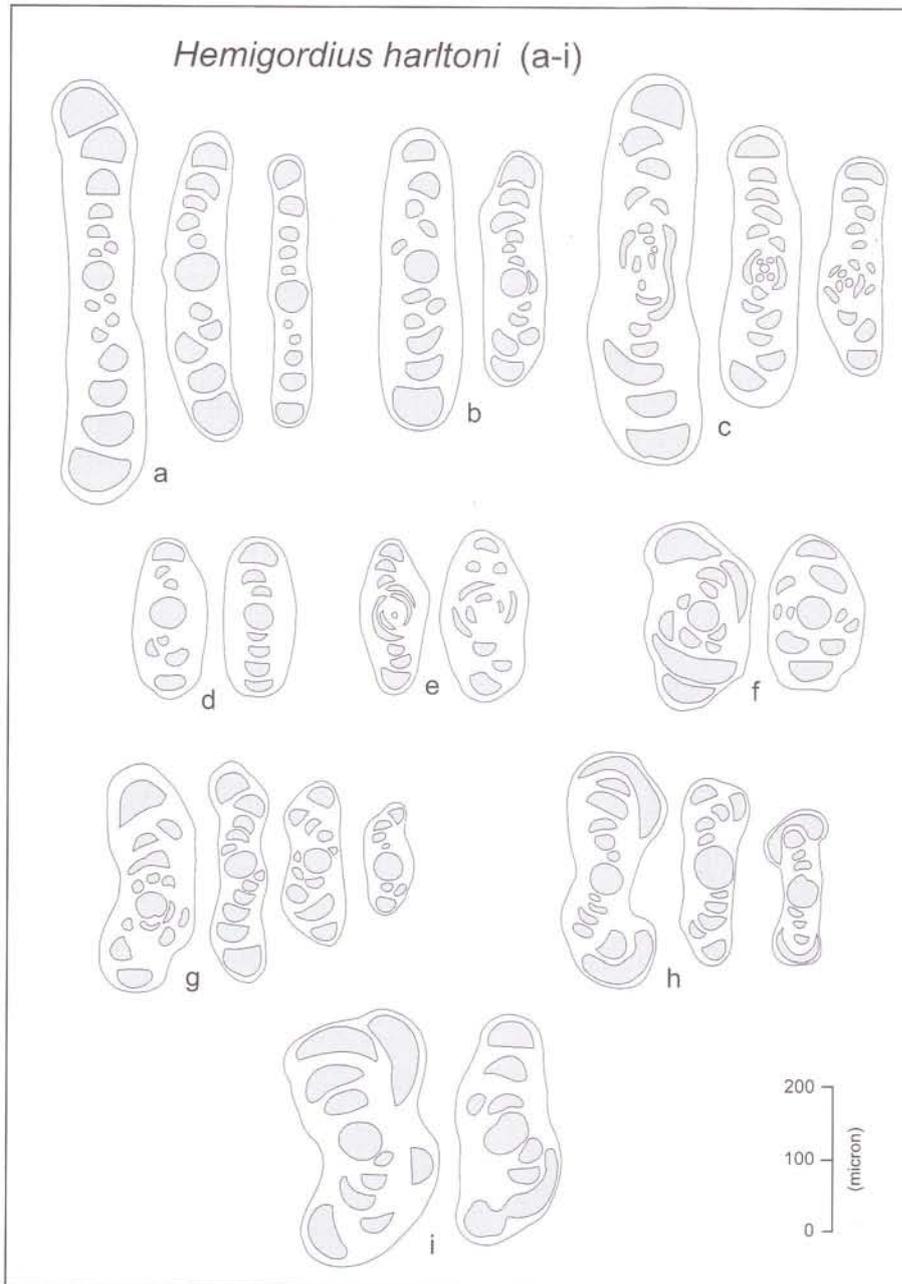


Fig. 2 - Morphotypes (a-i) of *Hemigordius harltoni*.

ral coiling) of inner whorls and a small proloculus (diameter: $5-10\ \mu$). In diameter/width plots (Fig. 3), these two morphotypes are distinctly separated from morphotypes a, b and c.

Lenticular to globular tests (diameter: $210-260\ \mu$; width: $130-140\ \mu$; form ratio $1.55-1.85$) with nearly streptospiral coiling of the **morphotype f** consists of 5 to $5\frac{1}{2}$ whorls and a relatively large proloculus (diameter: $40\ \mu$) (Fig. 2). The diameter/width plot of the morphotype is also distinctly separated from those of discoidal morphotypes (Fig. 3). The morphotype f differs from lenticular morphotypes d and e in having a smaller form ratio and more irregular coiling.

Morphotypes g and h (Fig. 2) are characterized by similar form ratios but a marked difference in coiling

mode. The morphotype g (diameter: $150-340\ \mu$; width: $60-110\ \mu$; form ratio: $2.3-4.3$) consists of irregularly sigmoidal 5 to 7 whorls and a large proloculus (diameter: $35-50\ \mu$). In the morphotype h (diameter: $200-340\ \mu$; width $60-80\ \mu$; form ratio: $3.1-4.9$) tests are composed of 4-6 oscillating to sigmoidal whorls with a marked deviation of the axis of coiling in the final whorl and a large proloculus (diameter: $40-55\ \mu$). Diameter/width plots of morphotypes g and h (Fig. 3) fall within the areal distribution of discoidal morphotypes a, b and c from which they differ by more irregular coiling.

Finally the **morphotype i** (Fig. 2) is characterized by lenticular tests with a rather irregular outline and irregularly coiled sigmoidal whorls (diameter: $310-360\ \mu$; width: $130-140\ \mu$; form ratio: $2.4-2.6$). Few oriented sec-

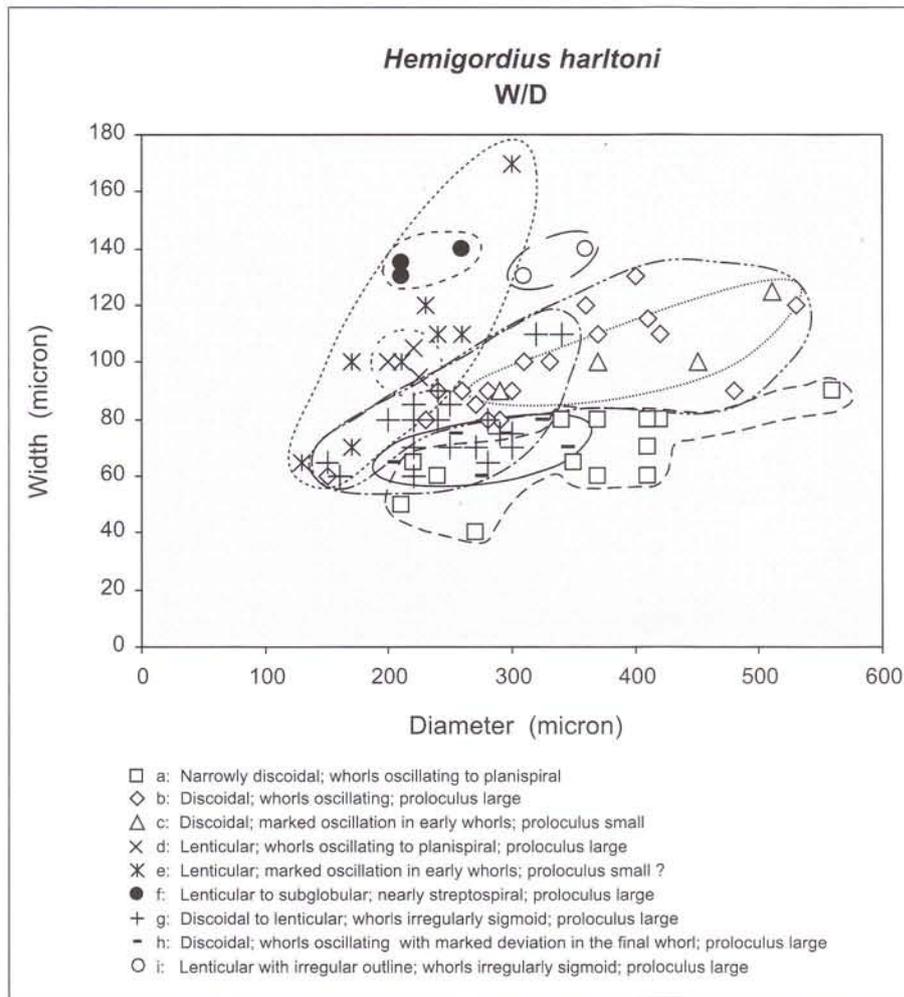


Fig. 3 - Width/Diameter plots of morphotypes (a-i) of *Hemigordius harltoni*.

tions have been recorded and the diameter/width plot indicates that this morphotype could be easily differentiated from discoidal forms (Fig. 3).

Although nine morphotypes, based both on coiling and form ratios, are readily distinguishable in *H. harltoni* population, three distinct morphotype groups can be characterized in diameter/width plots (Fig. 3). These are narrowly discoidal (morphotype a), discoidal (morphotypes b, c, g, h) and lenticular (morphotypes d, e, f, i) populations. In samples containing more than 300 individuals (for example borehole 1-NO-1-AM, core 811; borehole 1-AM-1-AM, core 2 and 4 and borehole 1-AM-2-AM, core 2) narrowly discoidal to discoidal forms dominate (more than 90% of the *H. harltoni* population). Lenticular forms (morphotypes d, e, f and i) are rare and occur sporadically in the boreholes of the Amazonas and Solimões basins.

According to traditional paleontologic practice, the distinct morphotypes of *H. harltoni* could be named as separate species. We eschew such a strictly typological approach, however, and instead regard *H. harltoni* as a polytypic species. Clearly, the convention of designating a single holotype specimen as the nomenclature standard-bearer is inadequate for communicating the range of

variability in a polytypic species. For polytypic species, it is necessary also to designate as paratypes a large number of variants and to discuss the relative frequencies of the morphotypes throughout the species' range

Although in the literature the variability in polytypic species is thought to result from different causes, such as, from ontogenetic development (Brummer et al. 1986) or from alternation of generations (Lee et al. 1991), the most evident one seems to be from variation in environmental conditions (Murray 1991), including seasonal morphological variations, as suggested by Pawlowski et al. (1994) in their taxonomic identification of recent foraminifera using ribosomal DNA sequences. Thus, we consider that polytypic species were produced in the geologic past in varying ecological conditions in which an organism lived and had certain "needs". The environmental stress probably affected individuals in such populations by producing different types of morphological features modifying, for example, mode of coiling. As far as these changes in the morphology wrought by the environment during the life of an individual did not become hereditary, this character was not transmitted to the next generation. Thus, these organisms could not breed; the derivation of a new species was retarded and these

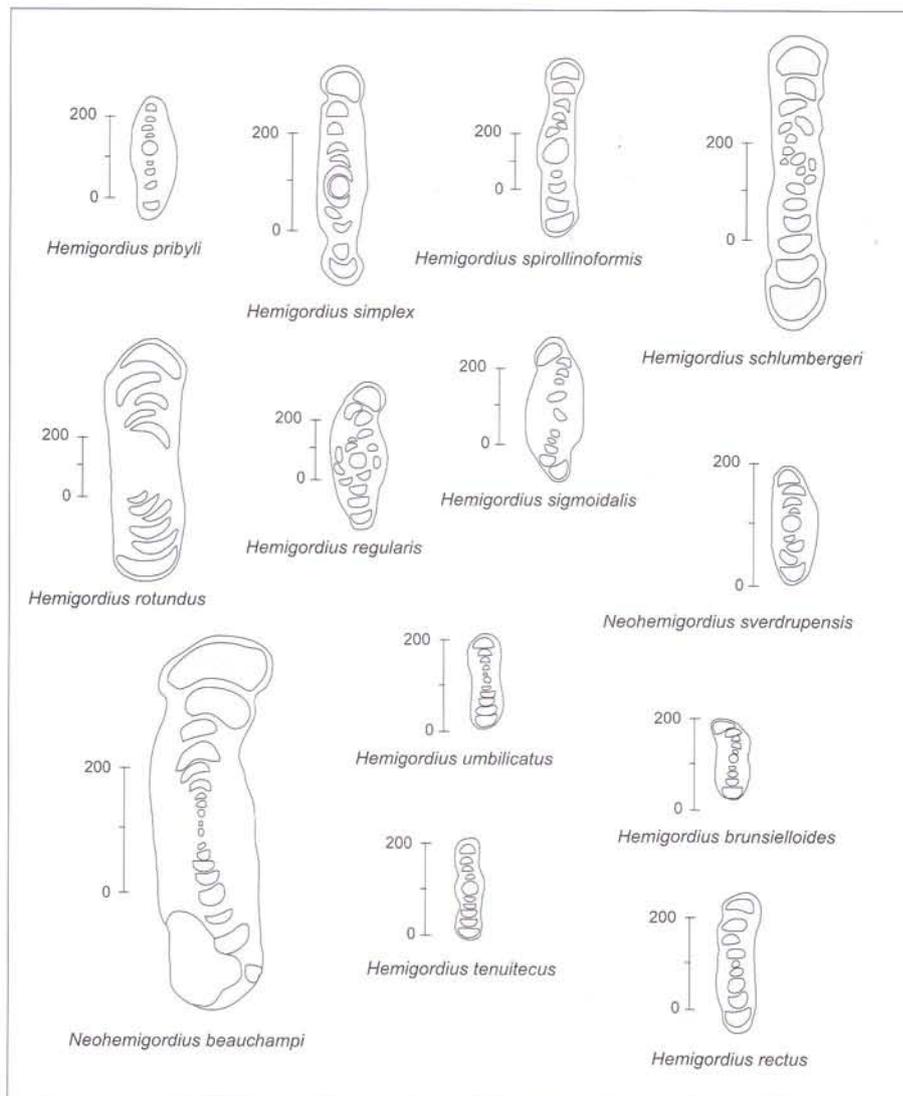


Fig. 4 - *Hemigordius pribyli* (a specimen from the type locality, Vašiček & R žička, 1957); *Hemigordius simplex* (Holotype, Reitlinger, 1950); *Hemigordius spirilliniformis* (Holotype, Wang, 1982); *Hemigordius schlumbergeri* (Pinard & Mamet, 1998); *Hemigordius rotundus* (Paratype, Wang, 1982); *Hemigordius regularis* (Holotype, Wang, 1982); *Hemigordius sigmoidalis* (Holotype, Wang, 1982); *Neohemigordius sverdrupensis* (Holotype, Pinard & Mamet, 1998); *Neohemigordius beauchampi* (Holotype, Pinard & Mamet, 1998); *Hemigordius umbilicatus* (Holotype, Kireeva, 1958); *Hemigordius brunsiielloides* (Holotype, Kireeva, 1958); *Hemigordius tenuitecus* (Holotype, Kireeva, 1958); *Hemigordius rectus* (Holotype, Kireeva, 1958).

individuals remained atypical representatives of the main population. In *H. harltoni*, these atypical representatives are grouped in morphotypes d, e, f and i because they never became dominant in the associations. In samples containing more than 300 individuals the relative abundance of these morphotypes never exceeds 2-3%. From

the rest of the population (narrowly discoidal and discoidal morphotypes a, b, c, g and h), morphotypes g and h could also be considered quite atypical with tests showing a considerable variation in the axis of coiling. The morphotype c is probably the microspheric generation of *H. harltoni*.

PLATE 2

All figures X 132

Fig. 1-41 - *Hemigordius harltoni* Cushman & Waters, 1928

1-2: Morphotype i; 3-5: Morphotype h; 6: Morphotype g; 7-9: Morphotype f; 12-13, 15: Morphotype d; 10-11, 14, 16-41: Undifferentiated specimens; 10: an attached test.
1-3, 5-7, 14, 35-36, 38-40: 2-CA-1-AM, core 7; 4, 8: 1-AM-6A-AM (borehole location close to 1-AM-1AM, fig. 1) core 13; 9, 11, 16-17, 19-21, 41: 1-AM-1-AM, core 4; 10, 13, 23, 32-34, 37: 1-TR-1-AM, core 14; 12: 1-AM-8-AM (borehole location close to 1-AM-1-AM, fig. 1), core 4; 15, 22, 29: 1-NO-1AM, core 811; 18: 2-UM-1-AM, 817 m; 24-28: 1-AM-2-AM (borehole location close to 1-AM-1-AM, fig. 1), core 2; 30: 2-PE-2-AM, core 4; 31: 1-AM-1-AM, core 2.

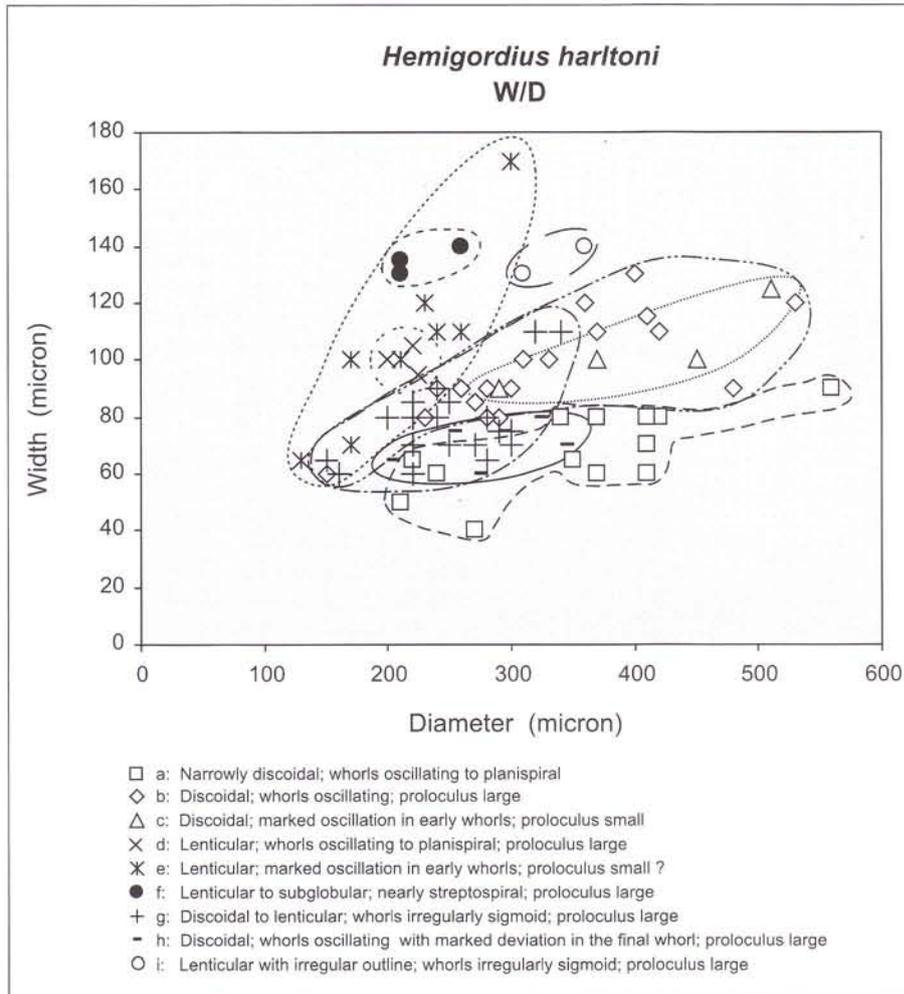


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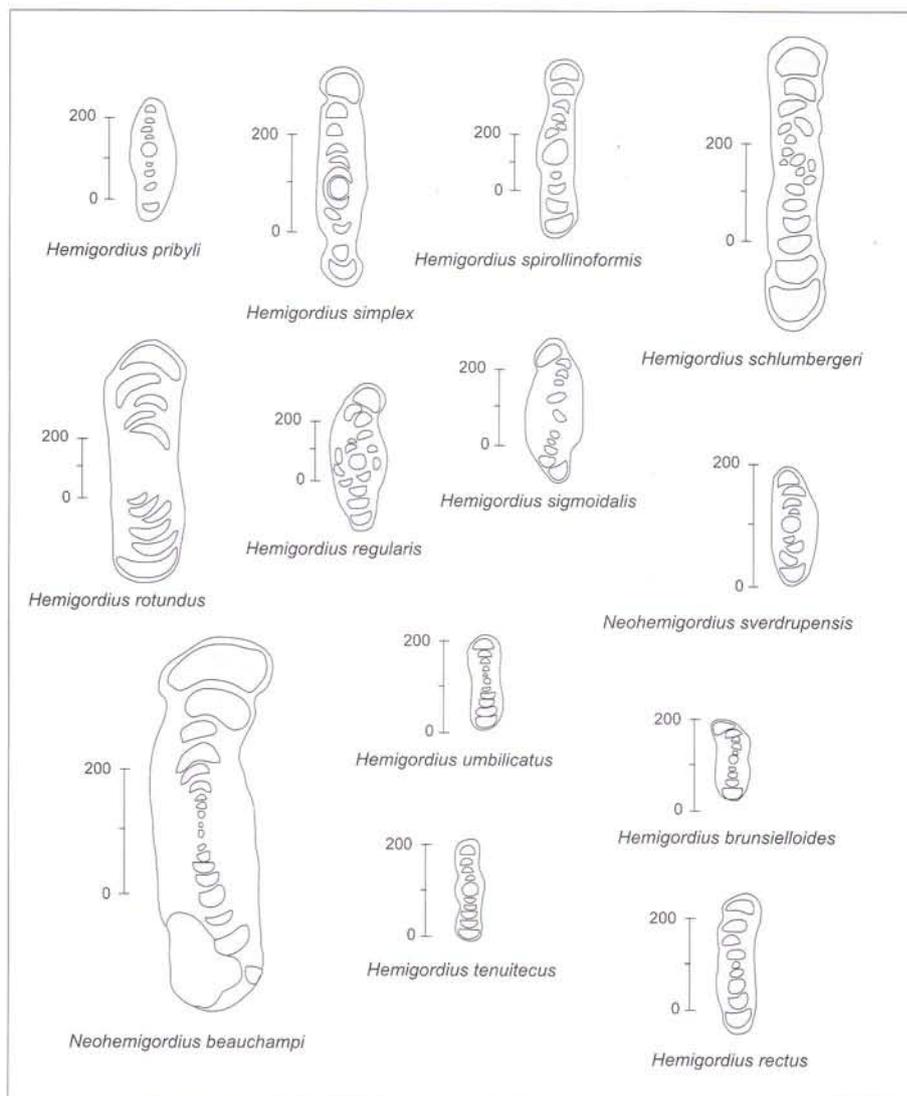


Fig. 4 - *Hemigordius pribyli* (a specimen from the type locality, Vašiček & Ržička, 1957); *Hemigordius simplex* (Holotype, Reitlinger, 1950); *Hemigordius spirilliniformis* (Holotype, Wang, 1982); *Hemigordius schlumbergeri* (Pinard & Mamet, 1998); *Hemigordius rotundus* (Paratype, Wang, 1982); *Hemigordius regularis* (Holotype, Wang, 1982); *Hemigordius sigmoidalis* (Holotype, Wang, 1982); *Neohemigordius sverdrupensis* (Holotype, Pinard & Mamet, 1998); *Neohemigordius beauchampi* (Holotype, Pinard & Mamet, 1998); *Hemigordius umbilicatus* (Holotype, Kireeva, 1958); *Hemigordius brunielloides* (Holotype, Kireeva, 1958), *Hemigordius tenuithecus* (Holotype, Kireeva, 1958); *Hemigordius rectus* (Holotype, Kireeva, 1958).

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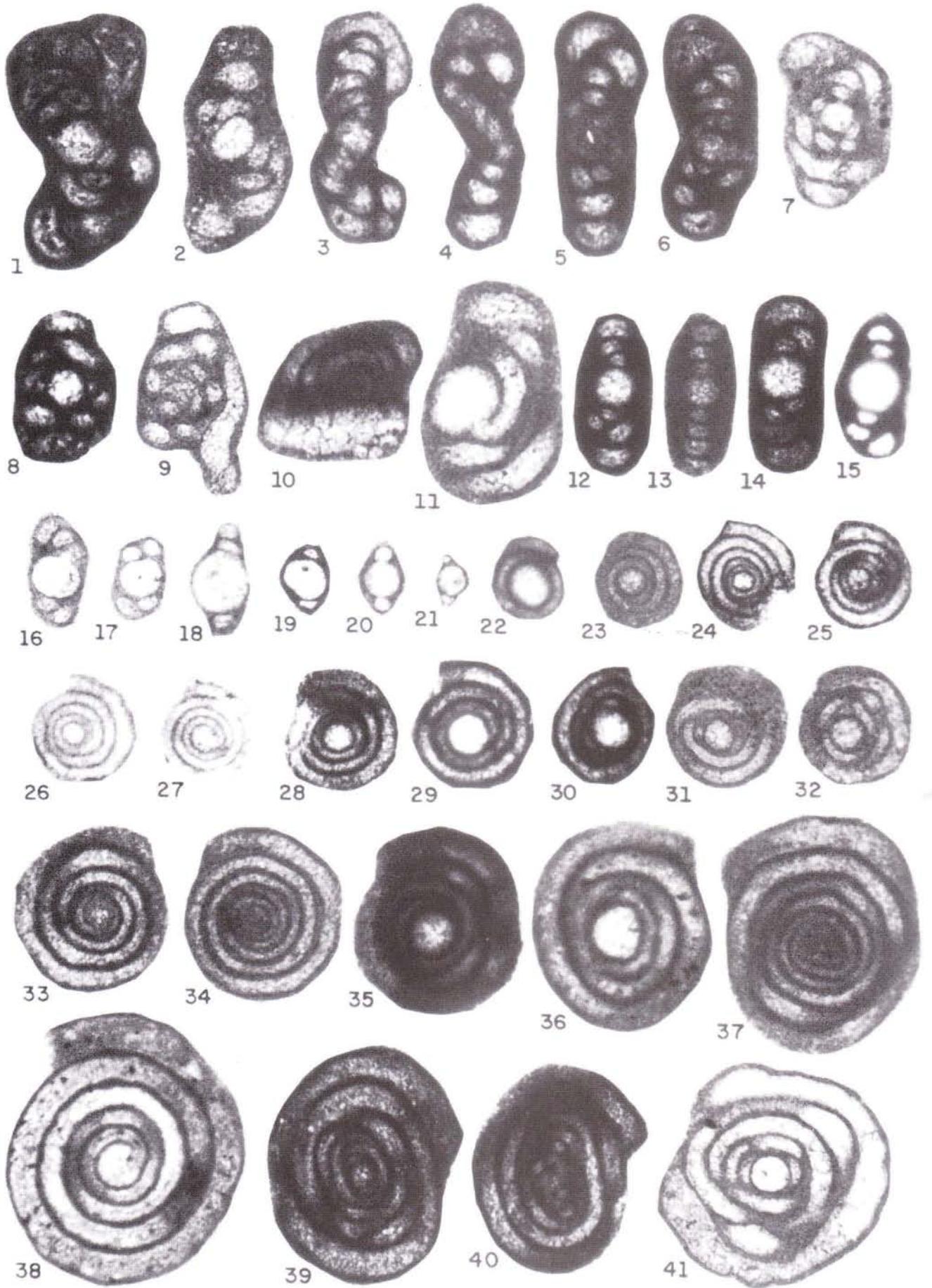
PLATE 2

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Fig. 1-41 - *Hemigordius harltoni* Cushman & Waters, 1928

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Remarks on some Carboniferous and Permian hemigordiopsid taxa

Carboniferous taxa

Hemigordius calcarea and *H. regularis*, two species described from the Pennsylvanian of Texas by Cushman & Waters (1928a) and Plummer (1930), respectively, are characterized by shells with initial streptospiral, then later planispiral whorls. We are not sure whether *H. calcarea* corresponds to one of the morphotypes of *H. harltoni* since it is a poorly illustrated and described species. As for *H. regularis*, it could be a morphotype of *H. harltoni*. Forms illustrated in Pl. 2, fig. 34 and 37 are surely sections of *H. regularis*.

Hemigordius livatus seems to be a distinct species. Cushman & Waters (1928a) described this species as being characterized by a compressed test with an acute or even slightly keeled periphery and irregular initial coiling followed by planispiral whorls. Since the sections of this species are not adequately known, specimens illustrated in Pl.3, fig 1-9 are questionably assigned to this species.

Hemigordius pribyli, described from the Namurian of Czechoslovakia by Vašíček & R. žička (1957) (Fig. 4), seems to be distinct from *H. harltoni*. According to illustrations of the type material, the weighted population is rather dominated by lenticular tests with convex sides and an elongate aperture observed on free specimens.

Hemigordius simplex and *H. spirolliniformis* (Fig. 4), both illustrated only in axial sections of their holotypes, were described from the Moscovian (Reitlinger 1950) and the Upper Carboniferous (Wang 1982), respectively. These species differ from *H. harltoni* by the evolute and suddenly enlarging last whorl, which is not the case in the morphotypes of *H. harltoni*. However, by considering the morphological variation in *H. harltoni*, we suggest the synonymy of these two species, with *H. simplex* having priority. *Hemigordius* sp. illustrated by Brazhnikova et al. (1967) from the Carboniferous is surely within the morphological variation of this plexus. In addition to its occurrence in the Carboniferous, *H. simplex* (reported as *H. cf. simplex*) was recorded from the Sakmarian of Afghanistan by Vachard & Montenat (1981).

Known from both the Carboniferous and the Per-

mian, the type species of the genus *Hemigordius*, *H. schlumbergeri* is characterized by discoidal tests with parallel flanks, initial glomospiroid, later evolute and planispiral coiling (Fig. 4). With this definition *H. schlumbergeri* is similar to the narrowly discoidal morphotype of *H. harltoni*. However, *H. schlumbergeri* differs from it by a prominent initial glomospiroid stage and more evolute nature of the planispiral portion of the test. *Hemigordius yuxianensis* Zheng, 1987 is a synonym of *H. schlumbergeri*. *Hemigordius schlumbergeri* has been recently correctly described or illustrated by Groves & Whalman (1997), Pinard & Mamet (1998) and Vachard & Krainer (2001a).

Described by Wang (1982) from the Upper Carboniferous, the type of *Hemigordius rotundus* is not a well oriented section to be used in taxonomical works (Fig. 4). However, this species seems to represent a different morphological trend in the Late Carboniferous, characterized by a low and broad second tubular chamber that slowly increases in height during ontogenesis.

Hemigordius regularis, described from the Upper Carboniferous of China by Wang (1982), is a species based only on the axial section of its holotype (Fig. 4). Intraspecific variability is not known. This form could be an atypical morphotype of a species characterized by a wider morphological variation including all small sigmoidal forms around the Carboniferous-Permian boundary. *Hemigordius xintanensis* Lin, 1984 could also be included within this plexus.

Early Permian taxa

Small hemigordiopsid species including *Hemigordius brunsielloides*, *H. rectus*, *H. umbilicatus* and *H. tenuitecus* (Fig. 4), described from the Lower Permian of the Donbass region by Kireeva (1958), are forms distinguished one from the other by minor morphological differences. Probably they all belong to the same population. *Hemigordius tenuitecus* has been lately described and figured by Pinard & Mamet (1998) (*Neohemigordius tenuitecus*, pl. 8, fig. 1-13) and Vachard & Krainer (2001b) ("*Arenovidalina*" cf. *tenuithec*a, pl. 5, fig. 2-6) from the Arctic Canada and Europe, respectively. Pinard & Mamet (1998) proposed the synonymy of *H. brunsielloides* and

PLATE 3

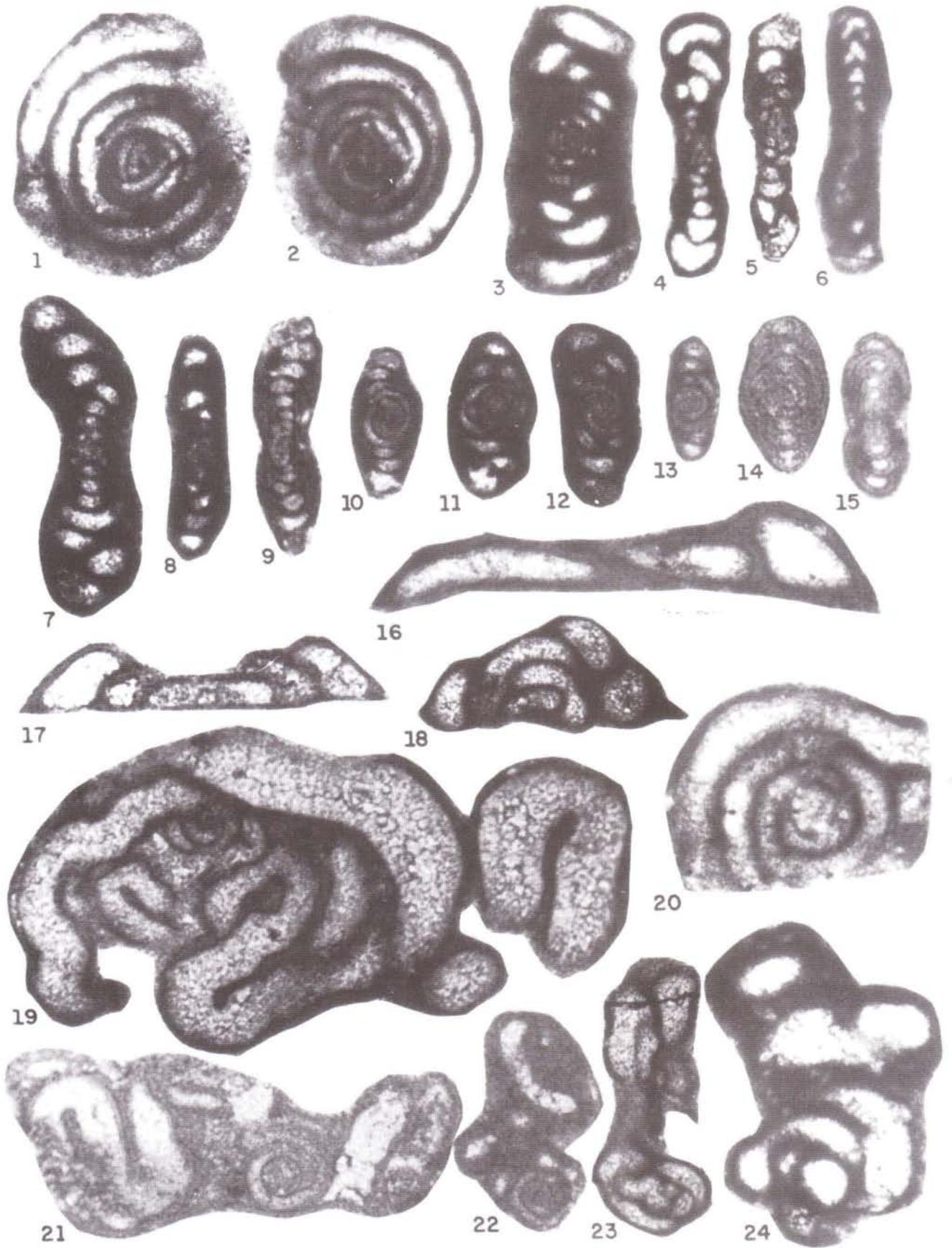
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Fig. 1-9 - *Hemigordius livatus* Cushman & Waters, 1928 ?

Fig. 10-14, 15 - ? *Hemigordius harltoni* Cushman & Waters, 1928 (Morphotype e).

Fig. 16-24 - Calcivertellidae (*Miliolina* associated with *H. harltoni*).

1-4, 8: 1-NO-1-AM, core 811; 5, 9: 1-MS-6-AM, 3070 m; 7, 11: 1-AM-6-AM (borehole location close to 1-AM-1-AM, fig. 1), core 3; 10: 1-AM-2-AM (borehole location close to 1-AM-1-AM, fig. 1), core 2; 12, 18: 2-CA-1-AM, core 7; 13: 2-MI-1-AM, 1140 m; 14: 1-TR-1-AM, core 14; 15: 1-NO-1-AM, core 794; 16, 20: 2-CA-3-AM, 1266 m; 19: 1-TR-1-AM, core 7; 21-22: 1-AM-1-AM, core 4; 23: 1-AM-1-AM, core 2; 24: 1-UR-1-AM, 2385 m.



H. umbilicatus under *N. ? tenuitecus*. *Hemigordius planispiralis* of Zheng (1987) is a form within the morphological variation of *H. tenuitecus*, thus a synonym of it. *Hemigordius* sp., illustrated from the Lower Permian of Iran by Lys et al. (1978) also belongs to *H. tenuitecus* population.

As we have stated earlier, *Hemigordius sigmoidalis* (Fig. 4), a species of Wang (1982) described from the Lower Permian of China, possibly belongs to the plexus of small sigmoidal forms around the Carboniferous-Permian boundary. Without studying the intraspecific variability of this plexus this species should not be used in taxonomical works.

The two species of hemigordiopsid foraminifera, *Neohemigordius sverdrupensis* and *N. beauchampi*, described from the Lower Permian of Arctic Canada (Pinnard & Mamet 1998), seem to be two well-established populations (Fig. 4). However, their assignment to *Neohemigordius* is doubtful. Within the morphological variation of *H. harltoni*, which we believe is a true *Hemigordius* species, forms quite close to outline of the holotype of *N. sverdrupensis* are present (compare morphotype d of *H. harltoni* in Fig. 2 with the holotype of *N. sverdrupensis* in Fig. 4).

The intention of Vachard & Krainer (2001b) to use a new name for the planispiral forms of hemigordiopsid foraminifera of the Upper Carboniferous and Lower Permian seems to be another problematic case. Although they used "*Arenovidalina*" temporarily following Baryshnikov et al. (1982) their illustrations are totally confusing in the generic classification of hemigordiopsid foraminifera.

The form illustrated in their Pl. 5, fig. 9 is planispiral but attributed to *Hemigordius* (*H. cf. permicus*). As for the illustrations in their Pl. 5, fig. 3 and Pl. 5, fig. 10 attributed to "*Arenovidalina*" cf. *tenuithecata* and *Hemigordius saranensis*, respectively, they do not exhibit important differences in generic character.

If one considers the morphologic spectrum of *H. harltoni*, these two species, as illustrated by Vachard & Krainer (2001b), could even be considered individuals of the same population.

Among four species described from the Artinskian of Urals by Grozdilova (1956), *Hemigordius ovatus* (Fig. 5), although its intraspecific variation is not known, is a well defined taxon with its oval profile and irregularly coiled initial whorls followed by whorls tending to become planispiral.

Other species of Grozdilova (1956), *Hemigordius longus*, *H. permicus* and *H. naliukini* are mostly discoidal forms with an oscillating axis of coiling (Fig. 5). These three forms are probably morphotypes of this large and discoidal hemigordiopsid trend in the Early Permian. *Neohemigordius longus*, as illustrated by Mamet (1996), is a specimen which belongs neither to this species nor to *Neohemigordius*.

Middle and Late Permian taxa

Evolutionary trends of *Hemigordius*-like foraminifera in the Middle and Late Permian interval split into various morphologic trends, each of which represents a distinct species or species group.

One of the major morphological trends is represented by discoidal forms consisting of oscillating whorls. *Hemigordius baoqingensis* Wang in Zhao et al. (1981) is the taxon with priority. *Hemigordius planus* of Pronina (1988) and Kotlyar et al. (1989), *H. harltoni* or *H. cf. harltoni* of Pantić (1963) and Vachard et al. (1993), *H. sp. 2* of Nguyen (1979), *H. irregulariformis* of Gargouri & Vachard (1988) (only the form illustrated in their pl. 2, fig. 6) and *H. gr. ovatus* of Pantić-Prodanović (1994) are probably forms which should be synonymized under *H. baoqingensis*.

Hemigordius sp. aff. *H. permicus* (Fig. 5), illustrated by Altiner (1981) and Zaninetti et al. (1981), is a trend not related with *H. permicus* of Grozdilova (1956) and is distinguished from it by much smaller size of the test and kidney-shape sections of the tubular chamber. This form should also be synonymized under *H. baoqingensis*.

As in the case of presence of both narrowly discoidal and discoidal morphotypes in *H. harltoni*, the newly described species *Hemigordius nikitinensis* from the Changxingian of northwestern Caucasus by Pronina-Nestell in Pronina-Nestell & Nestell (2001) is considered as a narrowly discoidal morphotype of *H. baoqingensis*.

The morphological trend consisting of wide discoidal forms with low and broad tubular chamber and convex lateral sides is represented by *H. guvenci* population (Altiner 1978) (Fig. 6) in the Middle-Late Permian. *Neohemigordius* sp. described by Kobayashi (1993) from Japan, *H. guvenci* described from the Djulfian-Dorashamian strata of Russia (Kotlyar et al. 1983) and *Okimuraites* ? sp. aff. *O. guvenci* described from the Middle-Upper Permian of South China (Ueno 2001) are surely synonyms of this taxon. Considering morphological variations and morphotypes of the Pennsylvanian *H. harltoni*, it is not tenable to attribute the *guvenci* population either to the genus *Neohemigordius* or to *Okimuraites*.

Forms with oval outline, sometimes with marked deviation of the ultimate or penultimate whorls, have been regrouped here under *Hemigordius irregulariformis* (Fig. 5). *H. (Midiella) irregulariformis* illustrated from the Midian of Russia by Kotlyar et al. (1983) and the Midian of Oman by Hauser et al. (2000), *H. permicus* from the Middle-Upper Permian of Iran by Jenny-Deshusses (1983) and *H. longus* from the Middle Permian of Serbia by Pantić-Prodanović (1994) are synonyms of this taxon. The form illustrated in pl. 2, fig. 5 of Gargouri & Vachard (1988) does not belong to *H. irregulariformis*. We think that this form is not even an *Hemigordius*.

Hemigordius sp. aff. *H. ovatus* (Fig. 5), illustrat-

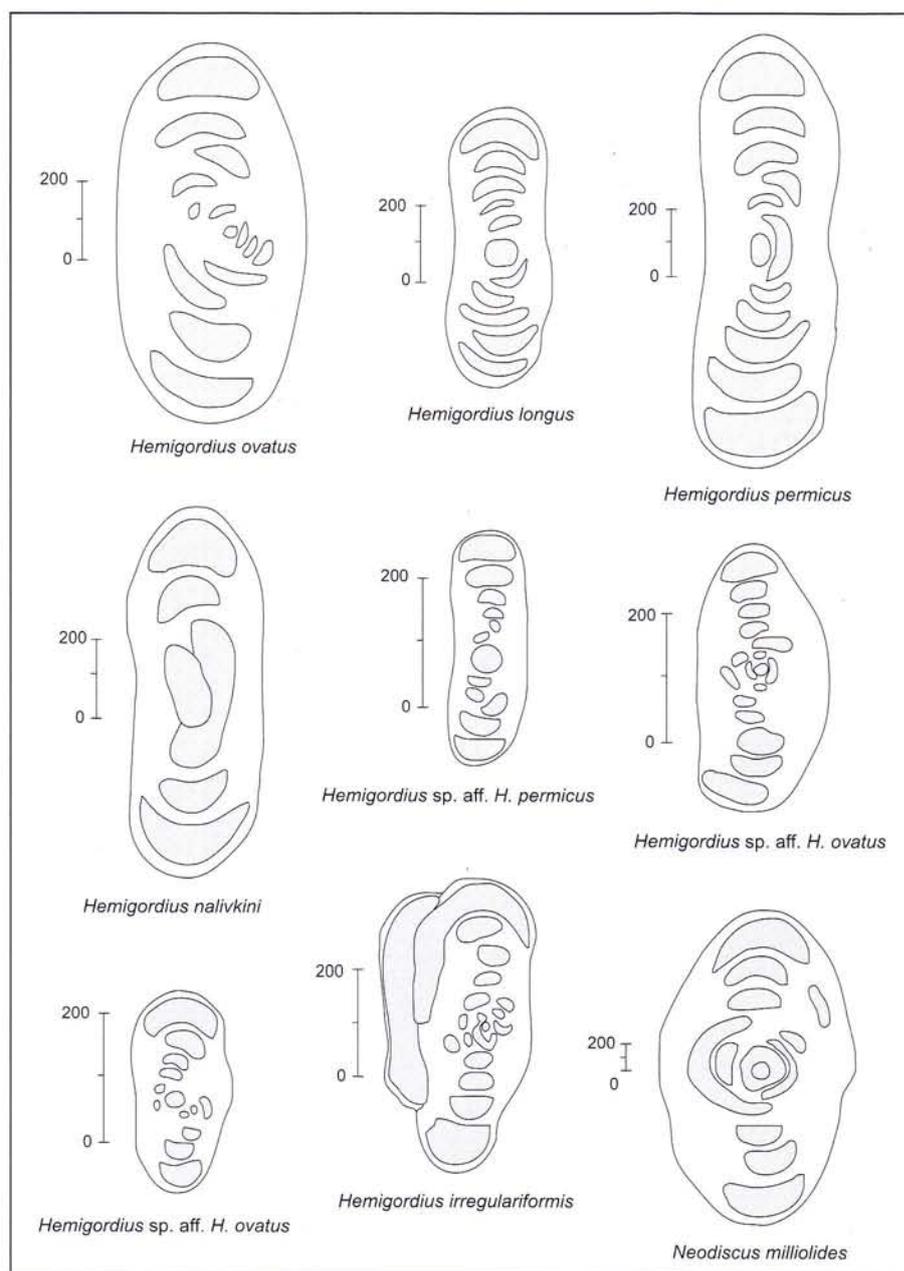


Fig. 5 - *Hemigordius ovatus* (Holotype, Grozdilova, 1956); *Hemigordius longus* (Holotype, Grozdilova, 1956); *Hemigordius permicus* (Holotype, Grozdilova, 1956); *Hemigordius nalivkini* (Holotype, Grozdilova, 1956); *Hemigordius* sp. aff. *H. permicus* (Altiner, 1981); *Hemigordius* sp. aff. *H. ovatus* (form illustrated in the second row, Altiner, 1981); *Hemigordius* sp. aff. *H. ovatus* (form illustrated in the third row, Zaninetti et al., 1981); *Hemigordius irregulariformis* (Holotype, Zaninetti et al., 1981); *Neodiscus millioides* (Holotype, Miklukho-Maklay, 1953).

ed and described from the Midian-Dorashamian interval of Taurides and the Arabian Platform by Altiner (1981, 1984), Zaninetti et al. (1981) and Köylüoğlu & Altiner (1989), differs from *H. ovatus* of Grozdilova (1956), first of all, by much smaller size of the test and by the kidney-shape tubular chamber instead of being low and broad in section. We note that, if this is the case, remembering the morphological variation in *H. harltoni* population comprising both discoidal (morphotypes a-c, g) and discoidal forms with marked deviation in the final whorl (morphotype h), forms assigned to *H. sp. aff. H. ovatus* could be within the specific variation of *H. irregulariformis*, introduced from the Taurus by Zaninetti et al. (1981) for hemigordiopsids with a marked deviation of the tubular chamber in the final whorl. The material given as *Midiella karinae* by Pronina-Nestell in Pronina-

Nestell & Nestell (2001) is surely a synonym of *H. irregulariformis* (compare this form with the holotype of *H. irregulariformis* given in Fig. 5).

In the Middle and Upper Permian, one of the well-established morphological trends consists of inflated forms with irregularly coiled early whorls followed by planispiral whorls. Described for the first time from Afghanistan by Lys in Lys & de Lapparent (1971), this form was correctly recognized in Turkey (Lys & Marcoux 1978; Altiner 1981, 1984; Zaninetti et al. 1981; Köylüoğlu & Altiner 1989) and in Cambodia (Nguyen 1979). Illustrations of Pantič-Prodanovič (1994, 1996) from Serbia are partly referable to *H. reicheli*. *Arenovidalina orientalis* and *A. ovoidea* of Sosnina (1978) are surely synonyms of *H. reicheli*. *H. reicheli evolutus*, introduced as a new subspecies (invalid taxon according to ICZN, species without

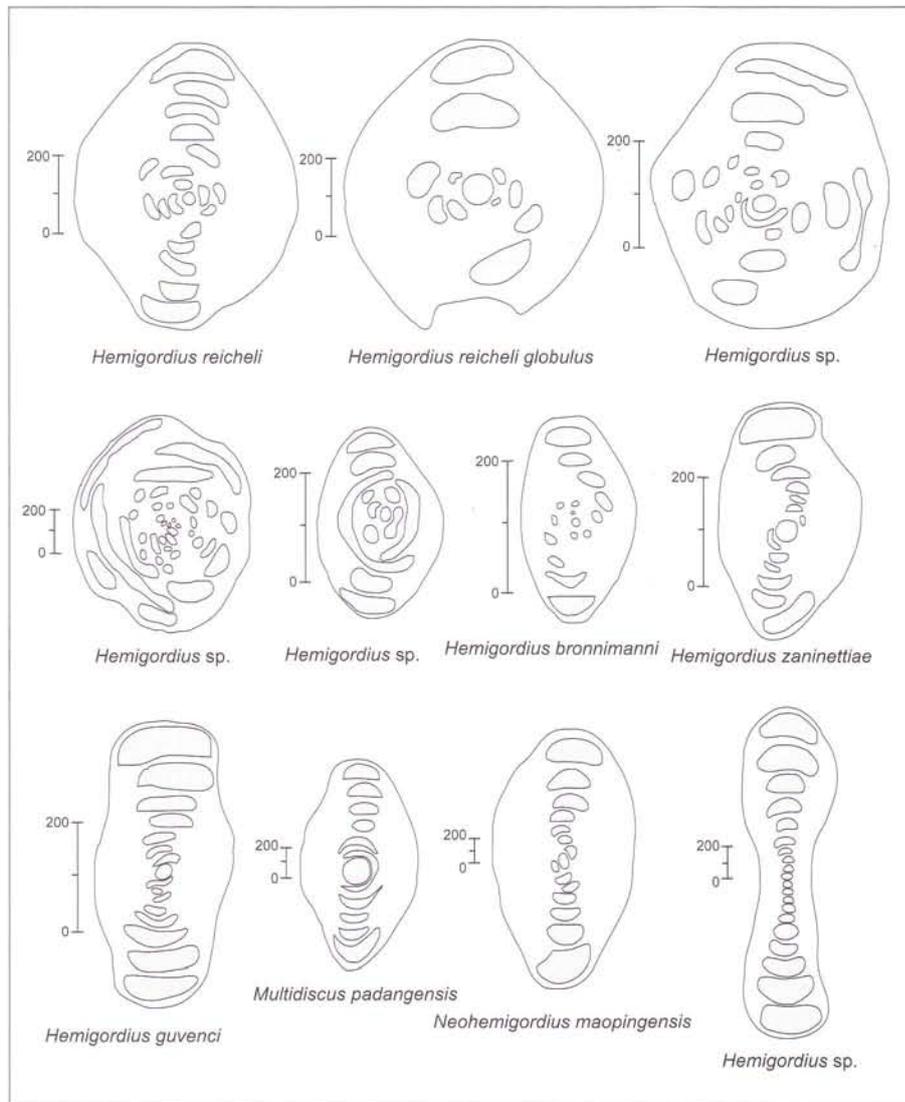


Fig. 6 - *Hemigordius reicheli* (Altiner, 1981); *Hemigordius reicheli globulus* (Holotype, Altiner, 1981); *Hemigordius* sp. (form illustrated in the first row, Altiner, 1981); *Hemigordius* sp. (first form from the left in the second row, Altiner, 1981); *Hemigordius* sp. (second form from the left in the second row, Altiner, 1981); *Hemigordius bronnimanni* (Holotype, Altiner, 1978); *Hemigordius zaninettiae* (Holotype, Altiner, 1978); *Hemigordius guvenci* (Holotype, Altiner, 1978); *Multidiscus padangensis* (Holotype, Lange, 1925; Miklukho-Maklay, 1953); *Neohemigordius maopingensis* (Holotype, Wang & Sun, 1973); *Hemigordius* sp. (form illustrated in the third row).

description) by Lys in Lys & Marcoux (1978) is not related to *H. reicheli*. This "taxon" used by Altiner (1981) as *Hemigordiopsis renzi evolutus*, with uniformly developed low tubular chamber and discoid to lenticular outline, should be assigned to the genus *Lysites* Reitlinger (type species: *Hemigordiopsis biconcavus* Wang, 1982) in Vdovenko et al. (1993).

In this study, considering the morphological variation in *H. harltoni*, we think that *H. reicheli* is also a polytypic species. In the eastern Taurides, although an inflated *H. reicheli* morphotype with early streptospiral and later planispiral whorls (Fig. 6) is the dominant and weighted population in this species, forms similar to illustrations of Altiner (1981) (Fig. 6, *Hemigordius reicheli globulus*, nomen nudum according to ICZN, form without description) and forms tending to become streptospiral but still resembling *H. reicheli* (*Hemigordius* sp. of Altiner, 1981, Fig. 6, form illustrated in the first row) are the other morphotypes recognized in *H. reicheli*.

Assigned to *Hemigordius* sp. (Fig. 6, the first form from the left in the second row) by Altiner (1981, 1984),

Zaninetti et al. (1981), Ciarapica et al. (1986), Panzenelli-Fratoni et al. (1987), Köylüoğlu & Altiner (1989) and Kobayashi (1997) or *Kamurana* sp. by Nguyen (1979), Vachard & Ferriere (1991) and Pronina & Nestell (1997) or *Neodiscus* ? or *Kamurana* ? sp. by Vachard et al. (1993), the entirely streptospiral hemigordiopsid population should be defined under a proper species and generic name. Widespread and occurring sometimes in rock-forming abundance both in the Northern and Southern Biofacies Belts of Altiner et al. (2000), this population probably evolved from the morphotype of *H. reicheli* tending to become streptospiral.

The sigmoidal tendency in the evolution of Middle and Upper Permian *Hemigordius*-like foraminifera is basically represented by two well established species, *Hemigordius bronnimanni* and *H. zaninettiae* described by Altiner (1978). In *H. bronnimanni* population (Fig. 6) the second tubular chamber is sigmoidally coiled with a rotation attaining 180°; however this coiling shows a certain irregularity depending on the morphological variability within the species. According to Vdovenko et al.

(1993), *H. bronnimanni* is the type species of the subgenus *Midiella* Pronina and *Midiella* is raised to the genus rank by Pronina-Nestell in Pronina-Nestell & Nestell (2001). At the moment of our research, except totally streptospiral forms that show a complete divergence from the general aspect of the genus *Hemigordius*, we do not consider that it is correct to erect new genera for different morphologic trends basically defined by coiling.

Hemigordius nanus described from China by Lin (1984) and *H. reicheli sigmoidalis* described from Turkey by Lys in Lys & Marcoux (1978) (invalid taxon according to ICZN, form without description) are synonyms of *H. bronnimanni*. In addition, several illustrations from Middle and Upper Permian including *H. bronnimanni*? of Jenny-Deshusses (1983), *H. sp.* of Noe (1987), *H. aff. ovatus* of Vachard et al. (1993), *Neohemigordius sp.* and *Hemigordius sp.* of Vachard et al. (1995), *H. (Midiella) bronnimanni* of Kotlyar et al. (1989) and *Midiella bronnimanni* of Pronina-Nestell in Pronina-Nestell & Nestell (2001) surely belong to *H. bronnimanni* population.

The other sigmoidal species, *H. zaninettiae* (Fig. 6), characterized by a lenticular profile with a rotation of whorls less than 90° and sometimes with a marked oscillation of whorls, is also a well established species introduced by Altiner (1978). *Hemigordius changxingensis* Wang in Zhao et al. (1981), *H. minutus* Pronina in Kotlyar et al. (1989) and Pronina-Nestell and Nestell (2001) and *Midiella karinae* Pronina-Nestell in Pronina-Nestell & Nestell (2001) (Pl. 1, fig. 15-holotype and fig. 16) are synonyms of *H. zaninettiae*. As stated in Pronina-Nestell & Nestell (2001) the holotype of *M. karinae* differs from *H. zaninettiae* (given as *M. zaninettiae*) by the presence of one evolute last volution and slightly different dimensions. However, as can be seen in the morphotypes of *H. barltoni*, such minor differences in the morphology do not justify the validity of a species.

In previous literature, *Hemigordius sp.* from Japan (Ishii et al. 1975), *H. ovatus minima* Grozdilova illustrated from Iran (Jenny-Deshusses 1983), *H. zaninettiae* of Sheng & He (1983) from China, *Neohemigordius cf. zaninettiae* of Vachard & Ferrière (1991) from New Zealand, *H. reicheli* (part), *H. padangensis*, *H. zaninettiae* and *H. ovatus* illustrated in Pantič-Prodanovič (1994) from Serbia and *Midiella zaninettiae* of Pronina-Nestell & Nestell (2001) from northern Caucasus are forms within the morphological variability of *H. zaninettiae*. The form attributed to *H. zaninettiae* in the thesis of Jenny-Deshusses (1983) is an unrecognizable section. *Hemigordius zaninettiae* should not be attributed to genera like *Neohemigordius* and *Midiella* whose definitions are based on arbitrary limits when compared with the genus *Hemigordius*.

In the Middle-Upper Permian of the Northern Biofacies Belt in Turkey one of the morphological trends in the evolution of *Hemigordius*-like foraminifera is apparently represented by discoidal forms of large size (*Hemigordius sp.*, Fig. 6, form illustrated in the third row) with

concave lateral sides and slightly oscillating or nearly planispiral coiling. The morphological variation in this trend is not known yet, however the well-developed profile suggests that this biconcave form could be the representative of a well-defined population.

Two distinct genera, *Neodiscus* and *Multidiscus*, described from the Middle-Upper Permian of Russia by Miklukho-Maklay (1953) are possibly the most evolved *Hemigordius*-like foraminifera owing to the presence of radially arranged fibrous structure in milioline-type wall. This structure, probably not diagenetic in origin, justifies the validity of these genera.

The type species of *Neodiscus* (*N. millioides*, Fig. 5) is characterized by an inflated test with irregularly coiled tubular chamber followed by planispiral whorls and is quite similar to *H. ovatus* from which it probably evolved.

Neodiscus scitus and *N. orbicus* of Lin (1984) are surely synonyms of *N. millioides* since they exhibit similar morphological features. The other valid species of *Neodiscus* are *N. grandis* (Ozawa 1925), *N. mirabilis* (Ueno 1992) and *N. speciosus* (Nikitina 1969).

The type species of the other hemigordiopsid in this group, *Multidiscus padangensis* (*Nummolostegina padangensis* of Lange, 1925) is a lenticular form displaying a nearly planispiral coiling with a slight deviation in early whorls (Fig. 6). However, the morphological variation in this species is probably much wider. The population contains forms with irregularly coiled early whorls or tests characterized by an oscillation of the coiling axis during the entire coiling.

Considering these variations the following species are considered synonyms of *M. padangensis*: *Arenovidalina crassa* Sosnina, 1977, *Hemigordius guangxiensis* Zhao et al., 1981, *Hemigordius wujipinensis* and *Multidiscus perforatus* Wang in Rui et al. (1984), *Hemigordius xarlashanensis* Wang, 1986 and *Multidiscus arpaensis* Pronina, 1986. In addition, *Permodiscus padangensis* Clément et al. (1971), *Hemigordius sp.* Nguyen (1979), *H. padangensis* Altiner (1981), *H. sp. 1* Jenny-Deshusses (1983) and Kotlyar et al. (1983), *Neodiscus maopingensis* Lin (1984), *Multidiscus sp. aff. M. gr. padangensis* Okimura et al. (1985), *M. sp. 1* Ueno (1992), *M. sp. A* and *B* Ueno & Sakagami (1993) and *M. sp.* Pronina & Nestell (1997) should be considered as *M. padangensis*. Biumblicate *Arenovidalina umbilicata* and inflated *A. rotunda* Sosnina (1978), compressed nautiloid-like *Multidiscus robustata* Lin (1978) and keeled *M. angulatus* Lin (1984) are probably the other valid species of *Multidiscus*. *Multidiscus ? tauridiana* Okuyucu (1999), described from the Lower Permian (Asselian), is probably not a *Multidiscus*. However, there is not any argument at the moment to assign this species to a different genus.

In the original definition of the genus *Neohemigordius*, Wang & Sun (1973) emphasized on three points to differentiate this taxon from *Hemigordius*: greater test thickness, symmetrically biconvex shape and planispiral

coiling. Having great test thickness and being symmetrically convex are not adequate parameters used to differentiate one genus from the other. In the morphological variation of a *Hemigordius* species, as in the case of *H. harltoni* (compare morphotype a and d or e) biconvex forms are present, in addition to discoidal forms. The planispiral coiling is not justified in the holotype of the type species of *Neohemigordius* (*N. maopingensis*). We observe that a marked deviation in the axis of coiling is present in the earlier whorls and the *maopingensis* population can not be considered as planispiral.

Although, in the type description of *N. maopingensis*, the wall structure is mentioned as gray to black, darker at the axial portion, lighter near periphery, the illustrations suggest that the aspect of the wall structure is quite similar to that of *Multidiscus*. If this is the case, *Neohemigordius* should be synonymized under *Multidiscus*, but not *Hemigordius*.

Conclusions

As it has been largely discussed in the text, *H. harltoni* is a polytypic species with several morphotypes. These morphotypes are grouped into two main assemblages. Dominant morphotypes are represented by narrowly discoidal to discoidal forms whereas lenticular to subglobular morphotypes are rare, sporadic and atypical. We interpret such morphotypes as groups of individuals with atypical morphological changes within *H. harltoni* population, wrought by the environment during the life. These morphotypes are never dominant in the associations and we consider them atypical and unsuccessful generations which could not succeed to breed. Thus, if one introduces a species in typological sense (without study-

ing morphological limits of a species whose definition is based on few specimens, sometimes only on the holotype) and such a taxon belongs to an atypical and unsuccessful generation, the recognition of the taxon becomes highly subjective and useless.

Most of the Carboniferous and Permian hemigordiosid taxa are poorly described and type definitions are based on few specimens. Considering morphologic variations and the polytypic nature of *H. harltoni* we question the validity of most of these species. Some are within the specific limits, thus synonyms of polytypic taxa which have wider morphological range (*H. simplex*, *H. tenuitecus*, *H. permicus*, *H. irregulariformis*, *H. reicheli* are examples of polytypic species in the genus *Hemigordius*). Since the environmental stress (unfavorable conditions) affecting these polytypic species might have occurred diachronously in different localities on the earth surface, similar-looking unsuccessful generations appear sporadically in different time intervals. Thus, the stratigraphic range given for the type material does not coincide with other records of the species.

We also conclude in this study that, among *Hemigordius*-like foraminifera, the genera *Hemigordius*, *Neodiscus*, *Multidiscus* are well defined. Instead, the genus *Neohemigordius* is a taxon which should be synonymized under either *Hemigordius* or *Multidiscus*. The decision on this synonymy should be made after the proper definition of the wall of the type species of *Neohemigordius* (*N. maopingensis*).

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