# Neospathodus and other Conodonta from the Saharonim Formation (Anisian-Ladinian) at Makhtesh Ramon, Negev, southern Israel

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**ABSTRACT**—63 conodont elements, referred to four multielement genera (*Neospathodus*, *Cypridodella*, *Ketinella* and *Ellisonia*) were recovered from the Upper Anisian-Lower Ladinian 'fossiliferous limestone' member of the Saharonim Formation, Makhtesh Ramon, Israel. The new form-species *Neospathodus shagami* sp. nov. is here described. Together with associated conodont elements, this species appears to show a close relationship to more advanced Gondolellaceans. Absence of true platform conodonts in the studied fauna may be due to paleoecological or phylogenetic factors.

### INTRODUCTION

Conodont elements were discovered in the Triassic rocks exposed at Wadi Rumman (Makhtesh Ramon) in the Negev region of Israel, then Palestine, at the same time as they were found in the nearby Sinai (see Fig. 1) (Eicher, 1946) though they were not described until much later (Eicher & Mosher, 1974). As that find may have represented the first conodont fauna unequivocally identified as Triassic, material from these outcrops merits special attention. Later studies of Triassic conodonts in Israel were by Sohn & Reiss (1964), Huddle (1970), Hirsch (1972, 1975, 1977), and Hirsch & Gerry, (1974).

In a recent survey of the foraminifera of the Ramon section (Benjamini, in prep.), conodont-like objects were observed in thin sections in Unit S1 of the Ramon Triassic, a rock unit spanning the Anisian-Ladinian boundary, from which conodonts had been previously recorded only from the uppermost level. In the present study, the original section at Har Gevanim, originally sampled by Druckman (1969, 1974) was revisited, and a sample from each limestone bed was systematically dissolved to recover the conodonts of this key unit. The beds chosen were those marked in the field by Druckman (1974) and the samples follow the original YD numbering system. Forty five limestone beds were sampled; only four yielded conodont elements. Dissolution was by 10% acetic acid solution, with the residue washed through a  $125 \mu m$  sieve.

#### UNIT S1 AND THE QUESTION OF ITS AGE

The Triassic Saharonim Formation of Makhtesh Ramon was defined and mapped by Zak (1963, 1968) (see Fig. 2). Druckman (1969, 1974) studied the Triassic of Ramon in detail and concluded, on litho-



Fig. 1. Location map showing position of Triassic exposures in Israel and neighbouring countries.

logical and petrographical grounds, that the Saharonim Formation, divisible into three members, represents deposition in shallow marine, lagoon and shoaling tidal





Fig. 2. Detail of Ramon area showing position of Har Gevanim section. Triassic outcrop area (with associated intrusives) stippled.

flat conditions. The lowermost part, the 'fossiliferous limestone' member (abbreviated S1), shown in Fig. 3, approximately 30m in thickness, represents the main transgressive phase and was deposited in an environment of normal salinity, mostly below wave base, and with a rich, normal marine biota. Megafossils from unit S1 have been studied in detail by Parnes (1962, 1965, 1975), Parnes *et al.* (1985), Lehrman (1960), and Brotzen (1956).

Biostratigraphy based on ammonites (Parnes, 1962, 1965, 1975) places the boundary between the Anisian and the Ladinian within the S1 unit. This placement is with some uncertainty because the ammonite species present in the unit, e.g. *Paraceratites (Paraceratitoides) brotzeni* Avnimelech in the lower part, taken to mark the Illyrian *trinidosus* Zone, and *Protrachyceras curionii* (Mojsisovicz) *ramonensis* Parnes, marking the Fassanian *curionii* Zone in the upper part of the unit, are local, endemic variants which are not directly comparable with European faunas.

## **CONODONT FAUNAS**

Conodonts recovered from the uppermost part of the S1 unit, are recorded in Table 1.

The species found by Hirsch (1972) from the upper part of the unit were as follows (generic assignments after Hirsch):

Pseudofurnishius murcianus Van den Boogaard Lonchodina muelleri Tatge Enantiognathus ziegleri (Diebel) Hibbardella magnidentata (Tatge) Hindeodella sp.

*P. murcianus* is characteristic of the Ladinian but possibly extends down to the Upper Anisian. The other

elements have not been illustrated by Hirsch (1972), but probably belong to the multielement to which *Pseudofurnishius* belongs. None of those auxiliary elements seems to be present in the current material.

In the present study, the original section studied by Druckman (1969, 1974) (Fig. 3) was revisited, and conodonts were recovered from several levels. Beds YD 67, 69 and 75, are from beneath a prominent ledge called the 'wavy limestone' by Zak (in Druckman, 1969) and contained the following conodonts:

Neospathodus shagami sp. nov. Cypridodella multielements Ketinella maxicavata Gedik

Ellisonia (?) sp.

The conodonts were taken from approximately the position of recovery of the lowermost of the Ladinian ammonites, Gevanites inflatus Parnes, but well below the position of the majority of the Ladinian ammonites including, among others, Gevanites awadi Parnes, G. altecarinatus Parnes, Israelites ramonensis Parnes, Protrachyceras curionii Mojs. ramonensis Parnes and P. wahrmani Parnes. Anisian ammonites from somewhat below the level of conodont recovery include Paraceratites (Paraceratitoides) brotzeni Avnimelech, indicating the trinodosus Zone of the uppermost Anisian. As nearly all ammonites were recovered from talus, the possibility that some may have weathered out from the inflatus level cannot be excluded, and the age of the conodont-bearing horizon must be placed as approximately astride the Anisian-Ladinian boundary.

Conodonts were recovered from YD 108 as well. At this level, the later Ladinian ammonites occur *in situ*. Conodonts present include the following:

*Neospathodus shagami* sp. nov. *Cypridodella* multielements *Ellisonia* (?) sp.

No platforms or elements of the *Pseudofurnishius* murcianus assemblage found by Hirsch (1972) were recovered though bed 108 is in the approximate position of, or slightly below, the level from which *P. murcianus* was derived. Indeed, nearly all the elements identified are here recorded from Israel for the first time.

Morphological nomenclature and systematics closely follow Robison (1981). Synonymy is somewhat abbreviated (for more complete synonymy see Mosher, 1968a, b and Gedik, 1975).

#### SYSTEMATIC PALAEONTOLOGY

Order Conodontophorida Eichenberg, 1930 Superfamily Gondolellacea Lindstrom, 1970 Family Ellisoniidae Clark, 1972 Genus *Ellisonia* Müller, 1956

**Remarks.** Only a single form-species found. Bears closer resemblance to illustrations of Ellisoniids than to the *Cypridodella* apparatus to which the other ramiform elements seem to belong. Wall appears more coarsely

m above base	sample number	conodonts
17	YD 67	Neospathodus shagami sp. nov.
18	YD 69	<i>Neospathodus shagami</i> sp. nov. <i>Cypridodella</i> multielements
25	YD 75	Ellisonia (?) Neospathodus shagami sp. nov. Cypridodella multielements Ketinella maxicavata Gedik
32	YD 108	<i>Neospathodus shagami</i> sp. nov. <i>Cypridodella</i> multielements
27- 37 (not precisely known	Upper part	(Fauna of Hirsch, 1972): Pseudofurnishius murcianus Van den Boogaard Lonchodina muelleri Tatge Enantiognathus ziegleri (Diebel) Hibbardella magnidentata (Tatge) Hindeodella sp.

crystalline; this may be an artifact of preservation but differs in this respect from the other elements recovered.

Ellisonia (?) sp. – Pb or Sb element (Pl. 1, fig. 1)

- 1958 Lonchodina spengleri Huckriede: 152, pl. 10, figs. 54, 55 (non 56), pl. 11, fig. 6, pl. 12, fig. 9, pl. 13, figs. 1, 6, 10, pl. 14, fig. 11.
- 1965 Lonchodina spengleri Huckriede; Mosher & Clark: 562, pl. 66, fig. 5.
- 1970 *Lonchodina spengleri* Huckriede; Bender: 513-514, pl. 3, fig. 12-15, 17.
- 1968 *Cypridodella spengleri* (Huckriede); Mosher: 922, pl. 113, figs. 18, 19, 20, 25.
- 1972 Hindeodella (Metaprionodus) spengleri (Huckriede); Kozur & Mostler: 16, pl. 7, fig. 11, pl. 10, fig. 4, pl. 15, fig. 1.
- 1975 Prioniodina (Flabellignathus) spengleri spengleri (Huckriede); Gedik: 146, pl. 7, fig. 23, 31, 33.

**Description:** Digyrate element with distal extremities broken off. Very narrow basal groove. No pit observed. **Occurrence.** 3 specimens, YD 75, Anisian-Ladinian boundary, one specimen, YD 108, Lower Ladinian.

### Family Xaniognathidae Sweet, 1981 Genus *Cypridodella* Mosher, 1968

**Remarks.** Each element belonging to this apparatus has been previously described as belonging to a distinct species, and indeed, genus. Though modern workers are now convinced of the necessity of placing associated forms within the same apparatus, the exact number of elements per apparatus and the relationship between the components of the apparatus remain unclear. An apparatus containing nearly all the elements found in the present association, and approximately the same age, is shown by Dzik & Trammer (1980) to be associated with platform conodonts of the 'Gondolella' mombergensis lineage, absent at Ramon. This complicates the taxonomic placement of these forms. Either the association described by Dzik & Trammer (1980) in fact does contain two distinct species, the unimembrate platform elements (absent at Ramon) and the Cypridodella seximembrate assemblage (present at Ramon), or else the same Cypridodella elements occur within different Neospathodus or Neogondolella species, differing only in Pa and perhaps Pb elements, in which case a single specific assignment for the other parts of the apparatus is not justified.

Cypridodella and Neospathodus usually occur separately, hence the hesitation by many authors to place them in the same multielement. Despite the small amount of material recovered from Ramon, the two form-genera occur together. However, the relative scarcity of Cypridodella vs. Neospathodus elements in our material, where they should be in fact some five times as abundant, argues for their occurrence in separate animals. Whether these are ecophenotypic variants, dimorphs, or distinct species is not known. Arguing for the other viewpoint, if the associated Neospathodus is not part of the Cypridodella apparatus, other Pa and Pb elements (spathognathodiform or ozarkodiniform) have not been found, though again the small amount of material must be taken into account.

To simplify their classification, the *Neospathodus* form-species is described separately, while the *Cypridodella* apparatus is left taxonomically open.

## Cypridodella sp. – M element (Pl. 1, fig. 2)

- 1958 Hindeodella multihamata Huckriede: 148, pl. 10, figs. 52, 53, pl. 12, fig. 23.
- 1968 *Hindeodella multihamata* Huckriede; Mosher: 925, pl. 114, fig. 19.
- 1970 *Hindeodella multihamata* Huckriede; Bender: 508, pl. 2, fig. 18, 20.
- 1972 Hindeodella (Metaprioniodus) multihamata (Huckriede); Kozur & Mostler: 16, pl. 7, fig. 2, 4.
- 1975 Prioniodina (Flabellignathus) multihamata (Huckriede); Gedik: 144, pl. 8, fig. 19.

**Description.** Bipennate, ramiform element, main denticle followed on posterior process by four smaller denticles and terminated by two larger ones. Anterior process much smaller than posterior, with four small denticles. Slight arch beneath main denticle. Narrow basal cavity.

Occurrence. YD 108, Lower Ladinian. One specimen and some fragments.

## Cypridodella sp. Sb element (Pl. 1, figs. 3-5)

- 1956 Hindeodella triassica Müller: 826, pl. 96, fig. 4, 5.
- 1958 Hindeodella triassica Müller; Huckriede: pl. 10, figs. 48, 50, pl. 14, fig. 8.
- 1965 Hindeodella triassica Müller; Mosher & Clark: 562, pl. 14, fig. 12, pl. 15, fig. 1-5.
- 1968 *Hindeodella triassica* Müller; Mosher: 925, pl. 114, fig. 22.
- 1970 Hindeodella triassica Müller; Bender: 510, pl. 2, fig. 22, pl. 3, fig. 1.
- 1971 Hindeodella (Neohindeodella) triassica triassica (Müller); Kozur: 10, pl. 2, fig. 10, 11.
- 1972 Neohindeodella triassica triassica (Müller); Kozur & Mostler: 24, pl. 1, fig. 24, pl. 4, fig. 13, pl. 7, fig. 12, 13, pl. 8, fig. 30, pl. 13, fig. 10, 13.

1975 Neohindeodella triassica triassica (Müller); Gedik: 136, pl. 6, fig. 12, 16, 23.

**Description.** Digyrate, arched ramiform element, with lateral process broken off. Prominent bump or angulation beneath the main denticle. Wide basal cavity. Denticles posterior to main denticle are all approximately the same size.

**Occurrence.** YD 75, Anisian-Ladinian boundary level. 3 well preserved specimens; some fragments.

Cypridodella sp. Sc element

- 1958 Prioniodella pectiniformis Huckriede: 158, pl. 13, figs. 18, 19.
- 1965 Prioniodella pectiniformis Huckriede; Mosher & Clark: 563, pl. 66, fig. 6.
- 1968 Prioniodella pectiniformis Huckriede; Mosher: 933, pl. 115, fig. 30.
- 1970 Prioniodella pectiniformis Huckriede; Bender: 525, pl. 5, fig. 7.
- 1972 *Hindeodella (Metaprioniodus) pectiniformis* (Huckriede); Kozur & Mostler: 15, pl. 5, fig. 1, 2, pl. 14, fig. 19, 23, 24, pl. 15, fig. 2, 4.
- 1975 Prioniodina (Flabellignathus) pectiniformis (Huckriede); Gedik: 144-5, pl. 8, fig. 22.

**Description.** Fragments of an elongate hindeodelliform element, apparently originally bipennate.

**Remarks.** This form occurs in fragments in the present material and is recognised by the straight, narrow bar, and denticles decreasing in size.

**Occurrence.** YD 69, 75, Anisian-Ladinian boundary level. 6 fragmented specimens.

### **Explanation of Plate 1** Conodonts from unit S1. Bar scale $100 \mu m$

- Fig. 1 Ellisonia (?) sp.
- Fig. 2. Cypridodella sp. M element.
- Figs. 3-5. Cypridodella sp. Sb element.
- Figs. 6, 7. Cypridodella sp. Sc element.
- Figs. 8, 9. Ketinella maxicavata Gedik. Sa element.
- Figs. 10-24. *Neospathodus shagami* sp. nov. Pa element; figs. 10-14, earlier variant, fused denticles, slight lateral bulge; figs. 14-18, 22, intermediate variant, free denticles, prominent bulge; figs. 19-21, later varient, with smaller number of denticles; figs. 23, 24, typical samples in oblique and basal views. Narrow basal and cavity and absence of platform can be observed. Holotype is fig. 22, from YD 75/1.
- Origin of specimens: YD 69 figs. 7, 10, 12-15, 17, 19, 20, 23, 24; YD 75 figs. 1, 3-6, 8, 9, 11, 16, 18, 21, 22; YD 108 fig. 2.



## Genus Ketinella Gedik, 1975 Ketinella maxicavata Gedik (Pl. 1, figs. 8, 9)

1975 *Ketinella maxicavata* Gedik: 128, pl. 5, fig. 9-11. **Remarks.** Absence of a symmetrical alate element from the *Cypridodella* apparatus would suggest this element should be placed there, in the Sa position. However, the triangular cross-section of the main denticle is specific to *Ketinella*, and the flaring basal cavity beneath it is not reported from *Cypridodella*.

**Occurrence.** YD 75, Anisian-Ladinian boundary level. 3 specimens (one has been lost subsequent to SEM observation).

Genus Neospathodus Mosher, 1968 Neospathodus shagami sp. nov. (Pl. 1, figs. 10-24)

**Derivation of name.** After Professor R. Shagam. **Diagnosis.** Form-species including *Neospathodus* with slight marginal bulge, narrow basal edge with non-flaring

posterior basal cavity, short denticles. **Holotype.** Shown in Fig. 3 (22). Deposited in BGU collection, marked BGU-YD 75/1 no. 1. Taken from Har Gevanim section, bed YD 75 (Druckman, 1969, 1974).

**Material.** 42 complete examples and some fragments; 50 in all.



Fig. 3. Columnar section of S1 unit at Har Gevanim, Makhtesh Ramon, showing position of conodont recovery in relation to ammonite – bearing subunits. After Druckman, 1974; Parnes, 1975.

**Description.** Segminate pectiniform element with slight marginal bulge at base of denticles, sometimes only on one side, in lateral view appearing as an incipient platform. Basal edge very narrow and blade like, with narrow, non-flaring posterior basal cavity extending back as a groove but ending approximately beneath third denticle from anterior end. Maybe slightly bowed. Relatively short, lightly striated denticles, 6-13 in number. May or may not have one larger (main) denticle, near posterior end. Denticles free or partially fused. Marginal ridge and narrow, keel-like basal edge present a distinctly battleship-like (as opposed to gondola-like) appearance.

**Dimensions.** Length,  $350-700 \,\mu$ m, width  $60-70 \,\mu$ m, height  $150-200 \,\mu$ m.

**Remarks.** Either unimembrate element or Pa element of *Cypridodella* multielement.

Similar to some variants of 'Gondolella' timorensis Nogami, but the latter species has a platform, albeit strongly reduced. The number of denticles in 'G.' timorensis is also considerably greater. There is also a fair stratigraphic gap, with 'G.' timorensis known from the Scythian to the earliest Anisian, and the present species, latest Anisian to Ladinian.

Corresponds closely to illustrations of "juvenile" stages of *Neogondolella navicula navicula* and related forms (Mosher, 1968b). However, some 50 specimens were recovered with no true platform developed, nor have any related Anisian or Ladinian platform elements been found previously in Israel. As it is not segminiplanate, it cannot belong to *Neogondolella*. Though in lateral view resembles some *Neospathodus* (*N. discreta* Muller, *N. homeri* Bender) it lacks flaring basal cavity of these segminiscaphate species. Establishment of a new form-species is therefore necessary.

The specimens recovered fall into three groups, which differ slightly in stratigraphic distribution:

a) Longer blades (6-700 $\mu$ m), with fused denticles, 10-13 in number. Main denticle the second or third from the posterior end. Marginal bulge may be absent from one or both sides. Present in YD 67, 69 (common); 75 (rare).

b) Free denticles, 9-12 in number. No real main denticle. Marginal bulge present. Present in YD 69, 75.

c) Free denticles, 6-9 in number. No real main denticle, but cusp-like posterior denticle may be larger than the others. Marginal bulge present. Found in YD 69, 75, 108.

These three groups form a complete gradational series, and could not be separated into subspecies; nor is such a separation justified on the basis of the amount of material available. There is some stratigraphic control over their respective appearance and relative abundance, with the shorter forms with fewer denticles being more common in the higher samples.

#### DISCUSSION

The new assemblage is well preserved and differs in important respects from other assemblages from Ramon and elsewhere in the Levant. Thus, despite the relatively small amount of material, attention must be paid to these divergences.

Outstanding among the recovered conodonts is *Neospathodus shagami* sp. nov., which is either a unimembrate element or the Pa element of the *Cyprido-della* multielement with which it is associated. As most Anisian and Ladinian assemblages in which both *Neospathodus* and *Cypridodella* elements occur contain platform conodonts as well, and as platform conodonts (*P. murcianus*) occur just above the recovery level, presence of *Neospathodus* to the exclusion of platform elements in the present material needs to be explained. Three tenable explanations have support in the literature: (1)*N. shagami* is present, and platform-bearing Gondolellaceans are absent, for palaeoecological reasons.

Seddon & Sweet (1971) and Druce (1973) suggested models for depth separation of conodont genera. Merrill & von Bitter (1976) suggest that separation may be by a variety of environmental factors such as energy and water chemistry. Clark (1981) and Sweet & Bergstrom (1981) both mention the palaeoecological separation between the Ellisoniid stock, to which Pseudo furnishius belongs, and the Xaniognathid stock, to which Neospathodus, Cypridodella and Neogondolella belong. The Ellisoniids are said to have inhabited shallow, inner shelf environments, while Xaniognathids are more characteristic of more basinal environments. Hirsch (1981) makes the same palaeoecological separation, with Pseudofurnishius placed in the neritic realm and Neospathodus in the epipelagic, though the former is considered by him also to be a Xaniognathid.

At Ramon, most of unit S1 contains a diverse molluscan fauna with abundant ammonites and nautilids, and from here the *Neospathodus-Cypridodella* fauna was derived, with only one questionable Ellisoniid element. At the top of unit S1, and from unit S2 upwards, presence of the *Pseudofurnishius* fauna of Hirsch (1972), which according to the palaeoecological model should inhabit inner, shallower shelf environments, is consistent with the lithological and palaeontological evidence (oolites, stromatolites, low-diversity molluscan bioherms, evaporites) for such shallower conditions.

Palaeoecological separation may additionally be invoked to explain absence of *Neogondolella* at Ramon, for example if *Neospathodus* were to inhabit epipelagic shelf environments and *Neogondolella*, more basinward facies. There is also the possibility that the new *Neospathodus* is only a shallower-water ecophenotype of a *Neogondolella*, and not a new species at all.

(2)*N. shagami* is a relict element of an earlier *Neogondolella* evolutionary lineage.

Forms close to Neospathodus shagami sp. nov. were

illustrated by Mosher (1968b) as juveniles of the 'Paragondolella' navicula navicula lineage, and a similar form was shown by Krystyn (1983) as a juvenile of 'Gondolella' eotrammeri, apparently an Anisian member of the same lineage. A possibility remains that the present assemblage is composed of juveniles of species from that lineage, perhaps in a palaeoecological habitat separate from that of the adults. Nevertheless, the large variability in size and number of denticles within the present material, and the fact that no platforms at all were found, lends credence to the interpretation that an adult form is in fact represented.

If there is in fact an evolutionary trend in which Scythian*Neospathodus* develops into*Neogondolella*, the current form may then be a predicted, but only now recorded, link in that lineage. However, while the current material is in fact from the latest Anisian-earliest Ladinian, the*Neogondolella* platform element was fully developed by the beginning of the Anisian.

Provinciality of the southern Tethyan region may provide a simple explanation (Hirsch, 1972, 1976). Scythian conodonts correlative with Alpine-Dinaric faunas of the Tethys were found in Lower Triassic strata in borings in Israel. Anisian ammonite faunas are, however, distinctly provincial, with endemic forms present in Ramon throughout the Anisian and into the Lower Ladinian. Ladinian faunas are primarily Sephardic, with correlation to southern Europe (Spain) and Africa, but not to the Alpine province. Pan-Tethyan faunal distributions were re-established by the Carnian.

According to this interpretation, the present fauna would be a relict element, derived from the Tethyan faunas of the Late Scythian but cut off from that region by the time of evolution of the *Neogondolella* platform. The platform element did not develop in the Ramon region and *Neospathodus* carried on in isolation to the base of the Ladinian. The fauna was superceded at the top of the S1 unit by the Lower Ladinian Sephardic *Pseudofurnishius murcianus* assemblage which also inhabited a slightly different habitat (Hirsch, 1972).

(3) N. shagami is an end-member of a Neogondolella evolutionary lineage.

There seems to have been some evolution within N. shagami within the upper S1 stratigraphic interval. Stratigraphically lower forms have fused denticles, 10-13 in number, but upwards this form becomes rarer, and variants with free denticles, fewer in number, and more pronounced lateral bulge become common, and exclusively present in the Lower Ladinian bed YD 108. This development is opposite to the sense of ontogeny in N. navicula as described by Mosher (1968b), in which the number of denticles actually increases in ontogeny. The sequence as found could represent a paedomorphic development, in which an adult feature (incipient platform) becomes established on forms with juvenile number of denticles, which upwards in the stratigraphy cease to increase in number in ontogeny as the parent species did.

A paedomorphic trend similar to that suggested at Ramon is reported by Dzik & Trammer (1980) in the convergence of end members of the *Neogondolella mombergensis*— *haslachensis* lineage with *Neospathodus*, in sequential samples from the Anisian to the Landinian of the Holy Cross Mountains of Poland. Several evolutionary pathways resulting in a similar trend of platform reduction (including the paedomorphic hypothesis) were described by von Bitter & Merrill (1980) in their study of 'naked' Gondolellids in Pennsylvanian conodont assemblages of the central U.S. A similar pathway was invoked for derivation of 'Gondolella' timorensis, a morphologically similar and possibly closely related form, from 'G' milleri (Nogami, 1968), in the Scythian.

One therefore cannot say whether *Neospathodus* shagami sp. nov. at Ramon is in fact a perfectly normal *Neospathodus* species, a locally preserved relict of a Scythian lineage which became more advanced elsewhere in the Tethys, or is itself an advanced form which has reverted to a juvenile, pregondolellid morphology. Further studies on the conodonts of the Israeli Triassic should provide answers to these questions.

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