

Gradual evolution of the Early Cretaceous marine gastropod *Rissoina* lineage in central Poland

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Kaim, A. 2002. Gradual evolution of the Early Cretaceous marine gastropod *Rissoina* lineage in central Poland. *Acta Palaeontologica Polonica* 47 (4): 667–672.

The evolutionary changes of the Early Cretaceous (Valanginian) marine gastropod *Rissoina* (*Buvignieria*) sp. from Wąwał (central Poland) show a pattern typical of the Ancient Lake Concept. Its morphology is stable during period of unstable conditions and starts to change gradually when the environment becomes stable. The linear character of the evolutionary changes of *Rissoina* sp. and lack of evolution among co-occurring gastropods suggests that the rate of evolution was controlled by intrinsic factors, not the environment.

Key words: Gradual evolution, gastropods, Cretaceous, Ancient Lake Concept, *Rissoina*, *Buvignieria*.

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Introduction

Both the Red Queen hypothesis (Van Valen 1973) and the Stationary Model (Stenseth and Maynard Smith 1984) claim that environmental change drives the evolution, biotic in the first case and abiotic in the second case. Most of the previously documented fossil lineages (see Dzik 1999 and references therein) show a rather gradual and linear evolution, irrespective of environmental change. Paradoxically, the changes in environment seem rather to hamper evolution (Dzik 1999). This pattern of evolution is explained by the Ancient Lake Concept (e.g., Gorthner and Meier-Brook 1985; Gorthner 1992) developed from the evolution of gastropod lineages in freshwater, long-lasting, extant and fossil lakes. The data documenting this phenomenon are still growing, but marine gastropods in contrast to those from continental environments, displayed no such pattern. The temporal changes of the morphological characters in the lineage of *Rissoina* (*Buvignieria*) sp. from the Wąwał section of Valanginian (Lower Cretaceous) clays in central Poland may be interpreted as an example of gradual (Ancient Lake) evolution.

Studied specimens are housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL).

Geological setting

The claypit at the village Wąwał, located two kilometers east of Tomaszów Mazowiecki, exposes a rock section of Valanginian age. According to Kutek et al. (1989), the section encompasses the early and part of the late Valanginian (Fig. 1) a duration of about 5 million years (Harland et al. 1990). Although the clay is quarried continuously, the section has never been completely exposed at one time.

In the Wąwał section, a single transgressive/regressive cycle is recorded. The lower, transgressive part of the section reveals unstable hydrological conditions reflected in several profound reorganisations of the faunas (Kaim 2001). The subsequent environmental change at Wąwał (beginning with sample L1, see Fig. 1 for sample numbers) probably corresponds to the continuing expansion of the Boreal sea but faunal assemblages still suggest shallow-water conditions near the photic zone (Kaim 2001). A further sea-level rise (early late Valanginian high stand) widened a connection with the Tethys (sample B1) across southern Poland. During that time the Tethyan ammonite *Saynoceras* replaced the Boreal *Polyptychites* (Kutek et al. 1989). In the middle part of the section (samples F2–A2), interpreted here as deposited in the early late Valanginian high stand the faunal dynamics stabilized and fossils are not numerous (Kaim 2001). With the sea-level fall, the hydrological situation again became unstable. The first signs of the shallowing event are observed in a narrow zone close to the top of unit 11 (sample C5). A much more pronounced expression of the shallowing is recorded at the base of unit 13 (H3–G3). There, both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values dropped abruptly (Kaim 2001), clay sedimentation was replaced by deposition of silt. The abrupt change in lithology occurred with changes in the composition of the fauna (gastropods, bivalves, ammonites, ostracods, and foraminifers; see Kaim 2001), e.g., the Tethyan ammonite *Saynoceras* was replaced by the Boreal ammonite *Dichotomites* (Kutek et al. 1989). This suggests a profound hydrologic change. It can be ascribed to a global low stand in the late *Saynoceras verrucosum* Zone as suggested by Hoedemaeker (1984) and Kutek et al. (1989). A little later (probably in the earliest Hauterivian) the sea retreated from the Wąwał area.

The gastropod lineage under study continued through most of the environmental changes observed at Wąwał.

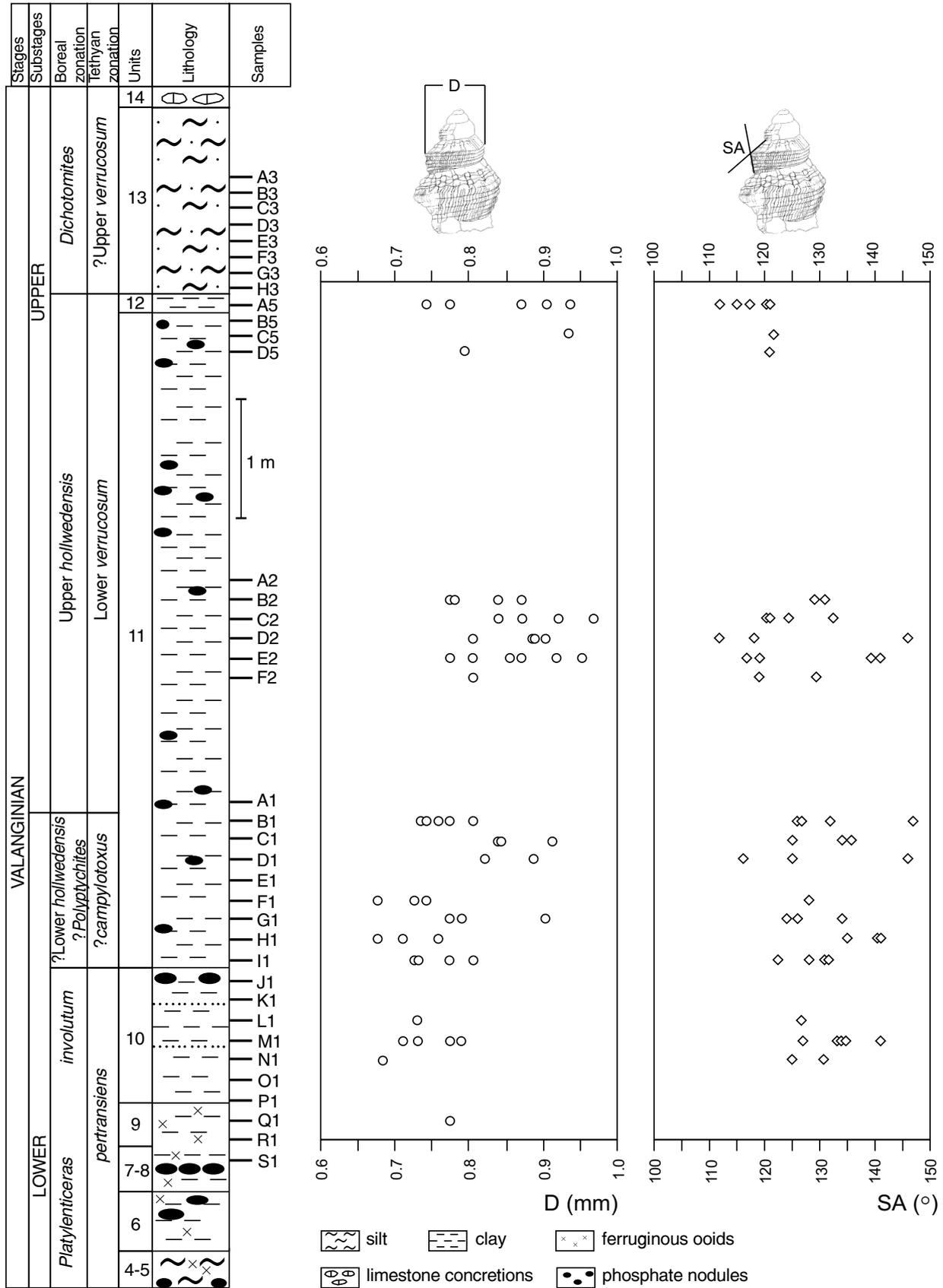


Fig. 1. Temporal changes in *Rissoina (Buvignieria)* sp. through the Wąwał section. The raw data of ecophenotypic parameter D (diameter at the first whorl of the teleoconch and shoulder angle) and parameter of presumed evolutionary importance SA (shoulder angle). The unsampled parts of section were inaccessible during fieldwork.

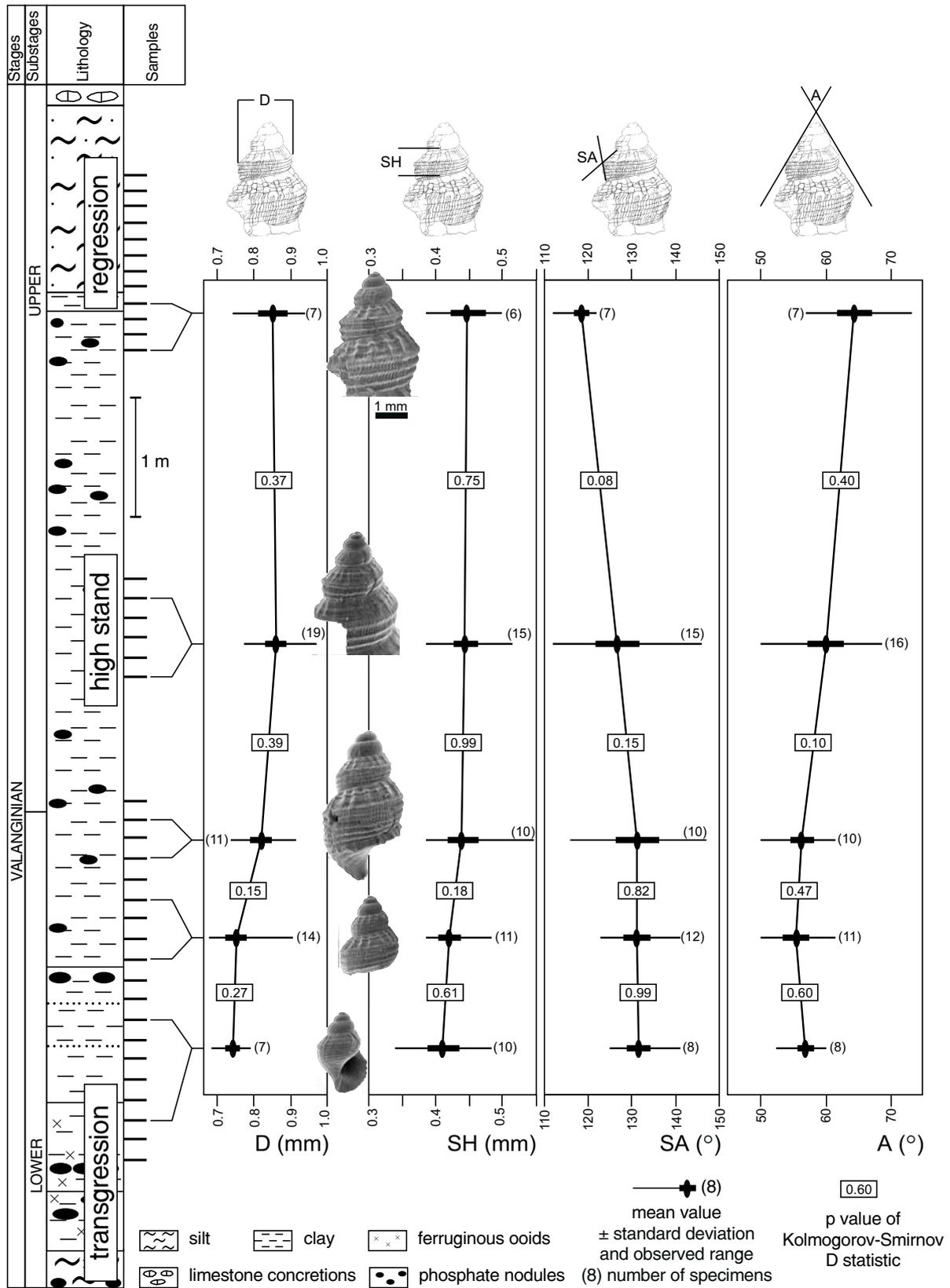


Fig. 2. Temporal changes of *Rissoina (Buvignieria)* sp. in the Wąwał section. The mean value, standard deviation, p of Kolmogorov-Smirnov D statistic, and observed range for diameter at the first whorl of the teleoconch (D), whorl height between abapical and adapical suture at the end of the first whorl of teleoconch (SH), shoulder angle (SA), and apical angle (A). Note that in the lower part of the section where the environment is unstable only the ecophenotypic parameters (D and SH) change whereas the parameters SA and A, both signals of morphological changes start to evolve after the environment stabilizes. The Kolmogorov-Smirnov D statistic counted with PAST software (Hammer et al. 2001) gives roughly the same results.

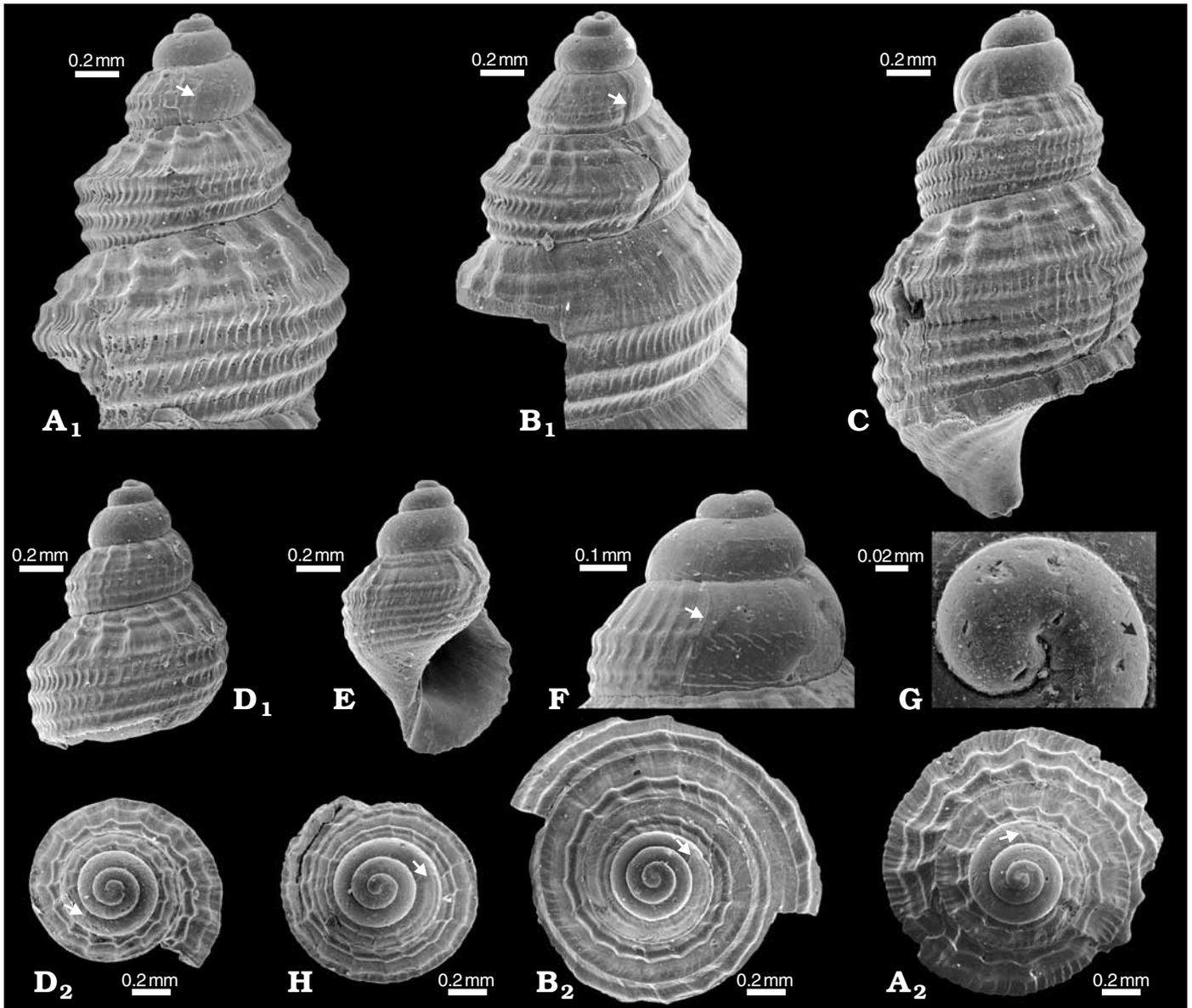


Fig. 3. *Rissoina (Buvignieria)* sp. from the Wąwał section. A. ZPAL Ga.9/44, sample A5, lateral (A_1) and apical (A_2) views respectively. B. ZPAL Ga.9/46, sample C2, lateral (B_1) and apical (B_2) views respectively. C. ZPAL Ga.9/52, sample C1, lateral view. D. ZPAL Ga.9/48, sample I1, lateral (D_1) and apical (D_2) views respectively. E. ZPAL Ga.9/49, sample M1, lateral view. F. ZPAL Ga.9/54, sample F2, lateral view of the protoconch. G. ZPAL Ga.9/43, sample L1, close-up of the protoconch 1. H. ZPAL Ga.9/53, sample C1, apical view. Black arrow shows the demarcation between protoconch 1 and 2, white arrows show the demarcation between protoconch and teleoconch.

Gastropod material

Three vertical series of samples (37 in total) have been collected from accessible parts of the section. The succession between these series was not exposed during sampling, resulting in two gaps. Each of the samples was about 2.5 kg in weight. They were washed with hot water on the sieve (mesh size 0.5 mm) and the fossils were picked from residues under the microscope.

The genus *Rissoina* d'Orbigny, 1840 belongs to the family Rissoidae Gray, 1847. The subgenus *Buvignieria*

Cossmann, 1921 is represented by several species from the Jurassic and Lower Cretaceous (see, e.g., Ponder 1985; Gründel 1998). *Rissoina (Buvignieria)* sp. is interpreted here as a single, undescribed species. The populations from the uppermost and lowermost samples may represent separate chronosubspecies (in the sense of Dzik and Trammer 1980) as the double standard deviation ranges of the shoulder angle (SA, see below) do not overlap. As the juvenile shells of this gastropod resemble to some degree juvenile aporrhoids, this gastropod was earlier identified as APOR-1 (Schröder 1995; Kaim 2001). A survey of Jurassic and Cretaceous rissoinids and aporrhoids leads to the

conclusion that this taxon should be included in Rissoinidae. Its protoconch (conical shape, oblique threads and opisthocytic demarcation with teleoconch) and teleoconch (angulation at the spiral cord) characters allow inclusion of the species in the subgenus *Buvignieria*. Detailed taxonomic treatment of this species will be published separately along with a revision of the Jurassic and Early Cretaceous rissoinids.

The shells of *Rissoina (Buvignieria)* sp. are a minor (about 1%, 174 shells in total) but almost constant component of the fossil assemblage of gastropods in the Wąwał section (see Kaim 2001). They appear in the first fossiliferous sample R1 and they have an almost continuous record through about 7 meters of the section until sample A5. After that they disappear together with several other gastropod species.

The gastropods are represented mainly by larval and juvenile whorls of the shell. The largest complete specimen does not exceed two whorls of the teleoconch. For this reason, in the majority of specimens, only the first teleoconch whorl was measured. To show the changes in morphology and size of the shells four parameters were used:

- diameter of the first whorl of the teleoconch (D),
- whorl height between abapical and adapical suture at the end of the first whorl of teleoconch (SH),
- shoulder angle (SA),
- apical angle (A).

First two parameters depict the changes in size of veligers and juvenile gastropods. The changes of these parameters seem to reflect ecophenotypic variability, expressing usually improvement or deterioration of environmental conditions (Moran 1999).

The shoulder and apical angles describe the changes in shell morphology. This kind of change is usually regarded as of evolutionary importance (compare Büttner 1982; Gorthner and Meier-Brook 1985; Reif 1985).

Raw data of diameter and shoulder angle are presented in Fig. 1. Because of the scarcity of well-preserved specimens the mean value and standard deviation were calculated for four arbitrary chosen sample sets (Fig. 2). The samples between sample sets yielded no specimens of *Rissoina (Buvignieria)* sp., (samples P1, O1, K1, A2, and B5) or the specimens were badly preserved (samples J1, E1, and A1).

Pattern of evolution in the Wąwał gastropod lineage

Among the numerous gastropod lineages represented in Wąwał only one, *Rissoina (Buvignieria)* sp. (Fig. 3), shows recognizable temporal changes. The evolution of *Rissoina* sp. in the Wąwał section can be divided into two parts. First phase of evolution took place during a sea-level rise when the hydrological conditions were unstable (see Kaim 2001).

Here the body-size (ecophenotypic) parameters D and SH show the same trend resulting in expansion of the protoconch volume (Fig. 2). Simultaneously the angular parameters SA and A are almost stable in this part of section. The enlargement of the veliger most probably reflects improvement of conditions for this species during the transgression. Similar disparity in the juvenile shell size was observed among living populations of gastropods, in more favourable conditions (e.g., subtidal environment) the hatched larvae are larger than those in less favourable condition (e.g., intertidal environment; Moran 1999).

In the middle part of the section, when the sea level reached a maximum, a period of relative hydrological stability occurred. The body-size (ecophenotypic) parameters (D, SH) are almost stable here (Fig. 2). In contrast, angular parameters (SA, A) started to evolve gradually from elongated forms into more isometric ones. Also the shape of the whorl had a tendency to change from oval to more angular with a strong spiral rib at the shoulder.

The following hydrological disturbance evoked most probably by a global lowstand in late *verrucosum* time (Hoedemaker 1984; Kutek et al. 1989; Kaim 2001), probably caused the disappearance of the species.

Conclusions

The case of *Rissoina (Buvignieria)* sp. provides evidence supporting the Ancient Lake Concept (Gorthner and Meier-Brook 1985), which claims that in fluctuating environments the morphology of organisms remains virtually stable whereas in stable environment the organisms tend to evolve gradually (see discussion in Dzik 1999). This phenomenon primarily documented from several long-lived lakes (Gorthner and Meier-Brook 1985; Reif 1985; Willmann 1985; Gorthner 1992) is also supported by several studies of lineages of other groups, e.g., ostracodes (Olempska 1989), conodonts (Dzik 1999 and references therein) and trilobites (Sheldon 1996). Although the number of such cases has increased, the cause of evolutionary change still remains unclear. The Red Queen hypothesis (Van Valen 1973) and Stationary Model (Stenseth and Maynard Smith 1984) both claim that environmental change drives the evolution, biotic in the first case and abiotic in the second. In the case *Rissoina* sp., there is no evidence in support of these hypotheses. No other gastropod species coexisting in Wąwał section with *Rissoina* sp. reveals any temporal change in its morphology. In the part of the section where the evolution of *Rissoina* sp. is best recorded, I did not find any traces of abiotic forces that could drive the evolution of the *Rissoina* sp. lineage. The problem in such cases is that the organisms are usually much more sensitive to any biotic or abiotic changes than a vulnerability of the fossil record to reflect the changes sedimentologically. On the other hand, the environmental changes recorded in the lower part of Wąwał section caused only ecophenotypic changes of the shell. The linear character of

the morphologic (evolutionary) changes in respect to time suggests rather an intrinsic control of their evolution rate as was suggested by Dzik (1999) for other examples of gradual evolution.

Acknowledgements

I am deeply indebted to Jerzy Dzik, Marcin Machalski, and Anders Warén for reviewing the early drafts of this paper. The paper greatly benefited from the reviews of David A.T. Harper, Alexander Nützel, and LouElla Saul.

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