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A Proposal for Taxonomic Re-Evaluation of *Vaccinites* Species from the Santonian Limestones of Southern Istria (Croatia)

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Key words: *Vaccinites*, Taxonomy, Cluster analysis, Santonian, Adriatic Carbonate Platform, Istria, Croatia.

Abstract

Rudists, especially members of the family Hippuritidae, were common dwellers on the Adriatic Carbonate Platform during the Late Cretaceous. Morphological elements (ligamental ridge, teeth, pillars, length of the contour around the inner margin of the outer shell layer and the ratio between this length and the distance between the sutures of the pillars) from the transverse shell sections permit different species to be defined within the family. Transverse sections of *Vaccinites* specimens from the Santonian limestones in southern Istria show different values of the angle between the teeth and the ligament ridge, between the ligamental ridge and the E pillar (P_2), and of the ratio between the length of the contour and the pillar suture distance. Cluster analyses (Ward's and Unweighted pair–group average methods) using measured elements, allowed the definition of three species groups from seventeen species at the beginning of study.

1. INTRODUCTION

Rudists are important macrofossils in the Upper Cretaceous of the Adriatic Carbonate Platform. Among them, hippuritids are common, particularly in the Santonian of southern Istria (MORO, 1997; MORO & ĆOSOVIĆ, 2000) where they have been used for detailed biostratigraphy (POLŠAK, 1965; POLŠAK et al., 1982). POLŠAK (1965, 1967) recognised seventeen species (Table 1) based on morphological characteristics (S and E pillars, shell thickness, visceral cavity and ornamentation).

Determination of the species within the family today is based on a combination of morphological elements (ligamental ridge, teeth, and pillars). The sector L–P_1–P_2, i.e. ligamental ridge and pillars of the lower valve (DECHASEAUX & COOGAN, 1969) are also very important for identification.

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The base for taxonomic re-evaluation is SKELTON's (1976) description (Fig. 1) of *Hippurites* and *Vaccinites*, involving evolutionary rotation of the myocardinal axis (SKELTON, pers. comm. 1973; in SKELTON, 1976), which was further developed by SIMONPIÉTRI & PHILIP (2000). The difference in angle, as a consequence of ventral expansion, produced a larger body cavity in *Vaccinites* in comparison with *Hippurites*.

Vaccinites shows different values of the angle between the teeth and the ligamental ridge, as well as that between the ligamental ridge and the P_1 pillar. Such angles have been based on different criteria for the description and determination of the hippuritids from the Southern Pyrenees (VICENS, 1992), Ostuni area (Italy – LAVIANO & MARESCA, 1992) and Boeotia (Greece – STEUBER, 1999).

According to VICENS (1992), angles between the teeth and the ligamental ridge may be useful for determining the genus and occasionally the group to which a species belongs. Also, beside other angles, the angle between the ligamental ridge and the P_1 pillar (LP2 in VICENS, 1992) could be useful for determining the species groups.

We have chosen the aforementioned two angles (Fig. 1) because they are the most prominent characteristic of the studied individuals, which flourished during a short time span, and in addition they have been found within the same facies (POLŠAK, 1965, 1967), as scattered individuals together with radiolitids in mud supported early Santonian floatstones (MORO, 1997; MORO & ĆOSOVIĆ, 2000).

Given the morphological variability of analogous living bivalves (e.g. oysters), among which more than a few species rarely co-occur in the same facies, the apparent high diversity of species recognised by POLŠAK (1967) may be questioned.

Our re-evaluation of *Vaccinites* species is based on biostatistics and on the field and laboratory experiences of the senior author. We are aware that statistical analysis is not a magic tool that will resolve the taxonomy of rudists. When specimens are incorporated in carbonates and it is quite difficult to extract them for determination, their identification at the species–group level using the simplest methods and tools in the field, has to be considered.

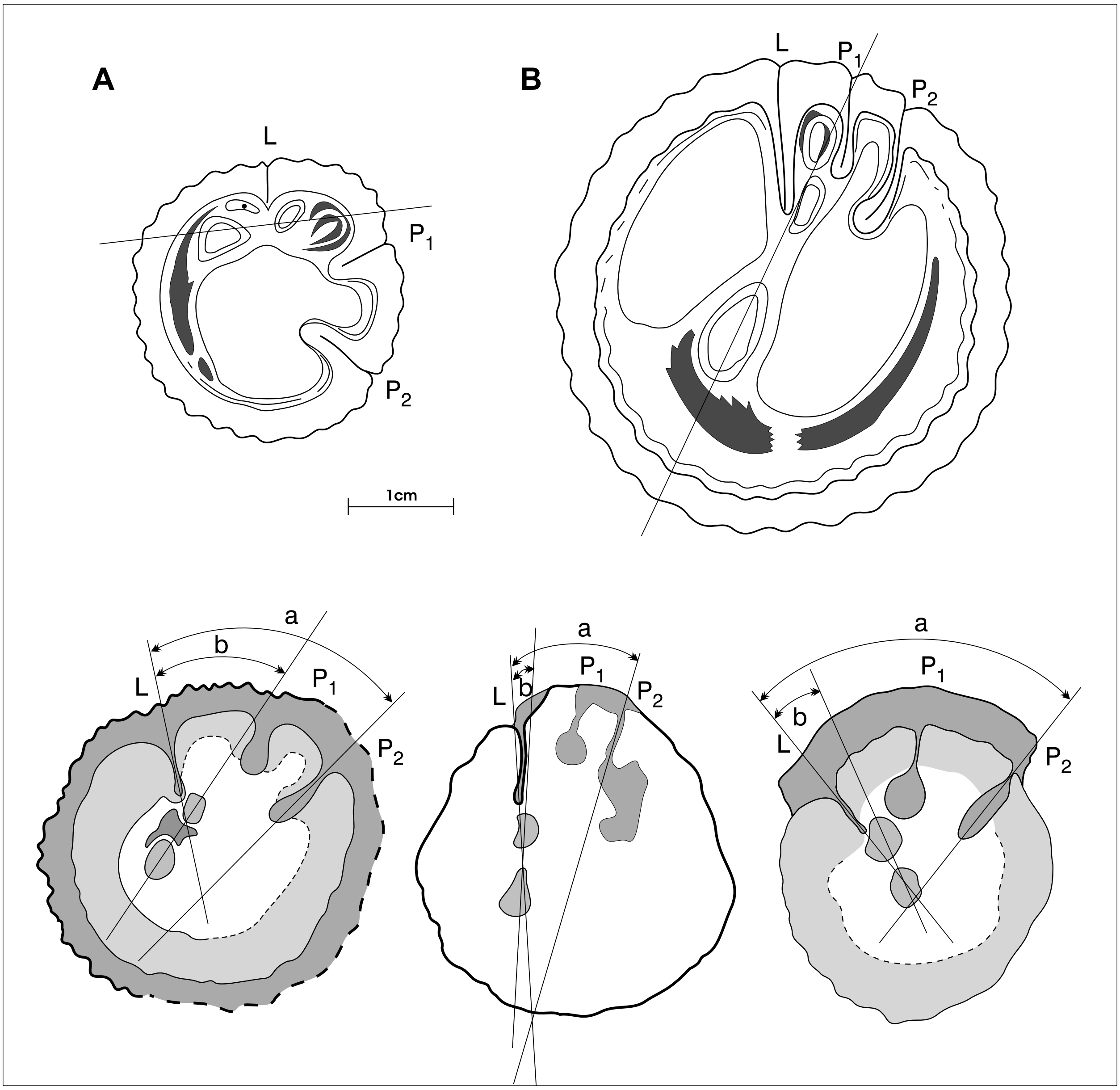

Fig. 1 Upper part of figure: transverse section of *Hippurites* (A) and *Vaccinites* (B) attached valves with rotation of myocardinal axis (from SKELTON, 1976). Lower part of figure: transverse section of *Vaccinites boehmi* (DOUVILLÉ), *V. atheniensis* (KTENAS) and *V. oppeli santoniensis* (KÜHN) from POLŠAK (1967) with L–P_2 (a) and L–T (b) angles. Transverse sections not to scale.

2. MATERIAL AND METHODOLOGY

All specimens have preserved ligamental ridges, as well as pillars. Teeth elements are in some specimens indeterminable probably due to calcite infilling of the shell interior, which has the same colour as the rest of the shell. Shell layers are poorly preserved. All specimens have been transversely sectioned. Here, we deal with broken specimens; all of them cylindrical in shape with the same diameters along the preserved part of specimens (see POLŠAK, 1967 – pl. 73, fig. 2; pl. 75, fig. 2; pl. 76, figs. 1 and 4; pl. 78, fig. 1; pl. 85, fig. 2). The constant diameters of the *Vaccinites* specimens allowed us to conclude that all specimens considered for this study were adults.

The measured structural elements are obtained from POLŠAK's (1965, 1967) transverse sections of the right valve of *Vaccinites* species (Fig. 1). They include the following:

- angle between the ligamental ridge and the E-pillar (L/P_2 in the further text, a in Fig. 1);
- angle between the ligamental ridge and the teeth (L/T in the further text, b in Fig. 1);
- inner diameter (RV interior, after LAVIANO & MARESCA,1992);
- length of the contour around the inner margin of the outer shell layer (U in the further text; STEUBER, 1999);

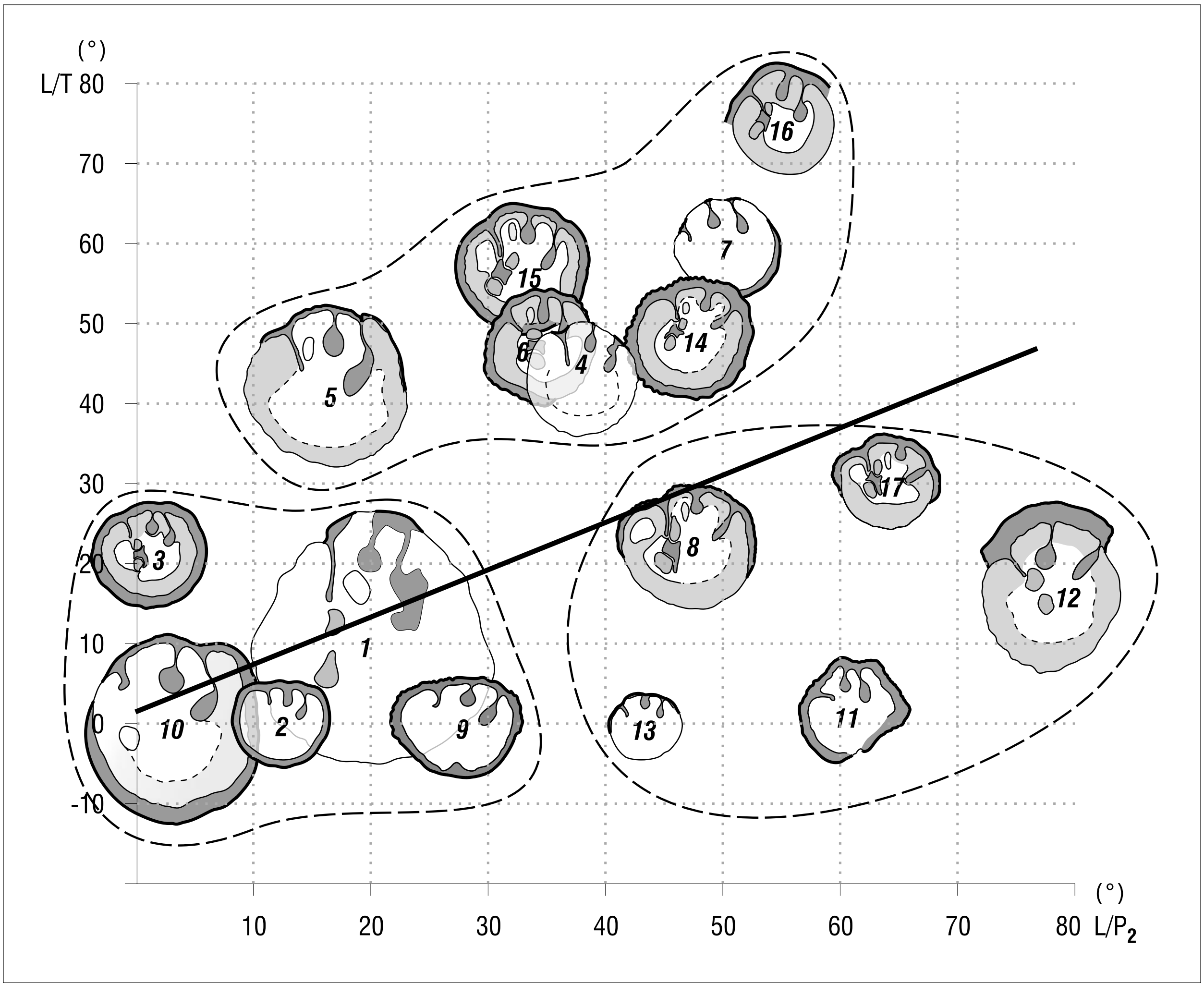

Fig. 2 Reduced major axis showing the relationship between L/P_2 versus L/T angles in *Vaccinites* species from southern Istria (after POLŠAK, 1965, 1967). The size of the transverse sections of the right valves of *Vaccinites* species are reduced with respect to their original size. Numbers attached to the transverse sections correspond to numbers given to species in Table 1. Dotted line encircles statistically determined groups.

– the ratio between the length of U and the distance between the sutures for P0–P2 (U/P0–P2 in the further text; STEUBER, 1999).

The angle L/P_2 is formed by straight lines which follow the general extension line of the ligamental ridge, i.e. which passes through the end of the ligament and the point where it intersects the inner diameter of the shell, and that which passes through the end of the pillar and the point where the P_2 pillar intersects the inner diameter of the shell (Fig. 1).

For measurement of the Ligament–Teeth (L/T) angle, the straight lines that follow the general extension of the ligamental ridge (as for L/P_2 angles), and that which passes through the centre of both teeth, was considered (Fig. 1). The measurements are displayed in Table 1.

Statistical analyses (35 specimens for L/P_2 and L/T and 17 for U and U/P0–P2) were calculated using the PAST software program (HAMMER et al., 2003). To avoid any possible dependency between variables, and to achieve the line of best fit, we plotted Reduced Major Axis (RMA) (Fig. 2). Unlike standard approaches, this model is invariant to the selection of which variable is portrayed on which axis, and to differences in variable type (MACLEOD, 2004).

The data were also subjected to cluster analysis. Cluster analysis is one of the most widely used and commonly understood multivariate analytical techniques in the palaeontological literature. It segregates entities (species, specimens, measurements) into “naturally occurring groups” and quantifies the between-group relationships (PARKER & ARNOLD, 1999). Hierarchical cluster analyses were calculated using the Ward Method with Euclidean distance and Unweighted Pair–Group Average Method with Euclidean distance.

Ward’s and Unweighted pair–group methods join two entities with the highest mutual similarity at each iteration. At each step, a potential new cluster that yields the lowest total Euclidean distance is formed. This continues until a single cluster remains. Recognition of “significant” clusters within a dendrogram are based on

		No. of specs.	L/P_2 min/max	L/T min/max	L/P_2 (°)	L/T (°)	d (cm)	Π (cm^2)	U (cm)	U/P0–P2 (cm)
1	*V. atheniensis*	3	18/22	6/8	20	7	4.1	52.8	84.6	6.0
2	*V. cornuvaccinum*	1			11		2.7	22.9	24.2	8.96
3	*V. taburni*	3		19/21		20	3.2	32.2	29.0	10
4	*V. giganteus*	2	37/37	41/47	37	44	3.1	30.2	36.1	8.804
5	*V. giganteus medulinus*	1			19	42	3.0	28.3	42.427	10.606
6	*V. salopeki*	5	30/40	42/48	35	45	2.7	22.9	32.2	7.318
7	*V. vredenburgi*	5	47/53	53/61	50	57	2.6	21.2	31.0	7.75
8	*V. inaequicostatus*	2	34/61	22/22	48	22	4.5	63.6	36.9	7.096
9	*V.* cf. *gosaviensis*	1			27		4.8	72.3	32.2	6.851
10	*V. kuehni*	1			2		4.3	58.0	43.75	8.75
11	*V.* cf. *kuehni*	1			62		2.8	24.6	27.0	6.923
12	*V. oppeli santoniensis*	2	77/77	15/15	77	15	4.5	63.6	46.5	5.81
13	*V. sulcatus*	1			43		2.3	16.6	20.1	6.931
14	*V. boehmi*	2	40/57	46/46	48	46	2.7	22.9	31.0	6.326
15	*V. extremus*	1			33	57	3.7	42.9	37.9	6.851
16	*V. anici*	1			55	74	2.9	26.4	33.5	6.836
17	*V. gosaviensis*	3	52/70	30/30	64	30	2.7	22.9	26.0	5.098

Table 1 The list of *Vaccinites* species from the Santonian limestones with measured parameters.

the shortest distance between paired *Vaccinites* specimens.

3. BIOSTATISTICAL RESULTS

Hierarchical cluster analysis (Ward's method in Fig. 3) on the ligament–E pillar (L/P_2), ligament–teeth (L/T), inner diameters, lengths of the contour (U) and the ratio between U and suture distance P0–P2, produced three main cluster groups.

The species *V. atheniensis* (1) (known as adult growth stage of *V. chaperi*; STEUBER, 1999), *V. cornuvaccinum* (2), *V. taburni* (3), *V.* cf. *gosaviensis* (9) and *V. kuehni* (10) represent the first cluster. The cluster combines species with L/P_2 angles from 2–27º, L/T up to 20º, U between 24.2 and 84.6 cm, and U/P0–P2 varying from 6.0 to 10 cm. The second cluster (Fig. 3) contains five species, *V. inaequicostatus* (8), *V*. cf. *kuehni* (11), *V. oppeli santoniensis* (12), *V. sulcatus* (13) and *V. gosaviensis* (17). The species gathered together are defined by the following characteristics: L/P_2 varying from 43 to 77º, L/T from 15 to 30º, U between 20.1–46.5 cm, and U/P0–P2 between 5.1 and 7.1 cm. The third cluster (Fig. 3) is composed of the following species *V. giganteus* (4), *V. giganteus medulinus* (5), *V. salopeki* (6), *V. vredenburgi* (7), *V. boehmi* (14), *V. extremus* (15) and *V. anici* (16). The cluster includes species with the L/P_2 angles between 19–55º, L/T values between 42 and 74º, the U between 31–42.4 cm, and the U/P0–P2 ranging from 6.3 to 10.6 cm.

The applied Unweighted pair–group method (Fig. 4) reveals the identical grouping of species.

The results emerging from the cluster analysis of the measured angles (L/P_2 and L/T angles, Fig. 5), identify three cluster groups: the first cluster (*V. giganteus* (4), *V. giganteus medulinus* (5), *V. salopeki* (6), *V. vredenburgi* (7), *V. boehmi* (14), *V. extremus* (15) and *V. anici* (16)), with an average L/P_2 value of 39.57º and an average value of L/T of 52.14º. The second cluster (*V. atheniensis* (1), *V. cornuvaccinum* (2), *V. taburni* (3), *V. cf. gosaviensis* (9) and *V. kuehni* (10)), combines species with the lowermost values of the angles, the average L/P_2 value of 12º and of L/T of 5.4º. The third cluster, (*V. inaequicostatus* (8), *V.* cf. *kuehni* (11), *V. oppeli santoniensis* (12), *V. sulcatus* (13) and *V. gosaviensis* (17)), is characterized by the largest disproportion of measured angles, the average value of L/P_2 around 59º and of L/T around 13º.

The Unweighted paired–group method of measured angles (Fig. 6) has resulted in the same grouping of species.

A particular difference in grouping of the seventeen species between linear graph (Fig. 2) and multivariate statistic analysis (Figs. 3–6) exists. The species with indefinite values of L/T or L/P_2 angles (for statistics we put value 0) are involved in this discrepancy.

4. MORPHOLOGICAL OBSERVATIONS

The determined groups of *Vaccinites* show certain degrees of morphological similarities.

Group I (Fig. 2, Table 2) contains forms with an elongated ligamental ridge, which are truncated at the tip. P_1 is pinched with an oval head. P_2 is pinched at its base and is longer than P_1. P_1 and P_2 could be located

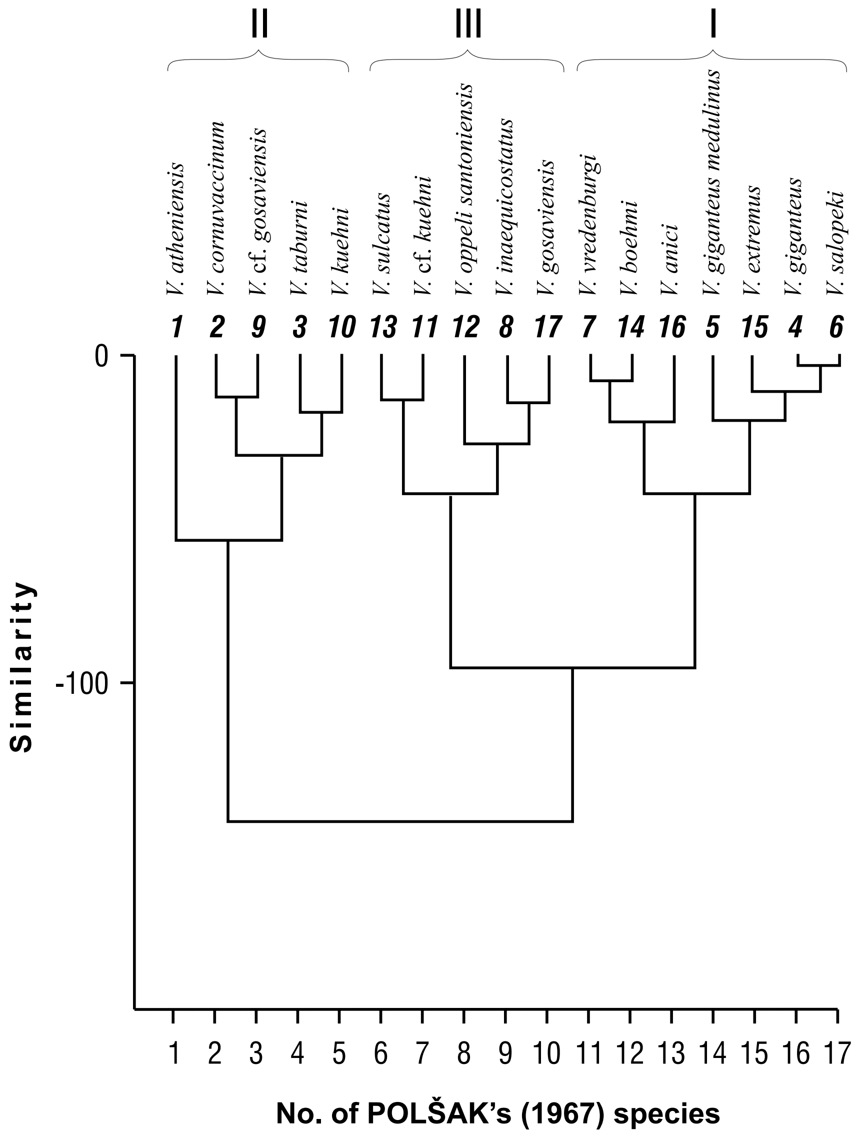

Fig. 3 Hierarchical cluster analysis (Ward's method) including all parameters for *Vaccinites* species from Santonian of southern Istria. Numbers I, II and III correspond to statistically determined groups.

	Group I	Group II	Group III
L/P_2 (°)	19–55	2–27	43–77
mean L/P_2 (°)	39.57	12	58.8
L/T (°)	42–74	7–20	15–30
mean L/T (°)	52.14	3.85	13.4
U	31–42.4	24.2–84.6	20.1–46.5
U/P0–P2	6.3–10.6	6.0–10	5.098–7.096
mean U	34.9	42.75	31.3
mean U/P0–P2	7.78	8.112	6.37
	V. giganteus	*V. cornuvaccinum*	*V. inaequicostatus*
	V. gig. medulinus	*V. taburni*	*V. o. santoniensis*
	V. salopeki	*V.* cf. *gosaviensis*	*V.* cf. *kuehni*
	V. vredenburgi	*V. kuehni*	*V. sulcatus*
	V. extremus	*V. atheniensis*	*V. gosaviensis*
	V.boehmi		
	V. anici		
Total no. of *sp.*	7	5	5

Table 2 Main characteristics of species groups recognized through statistical analyses.

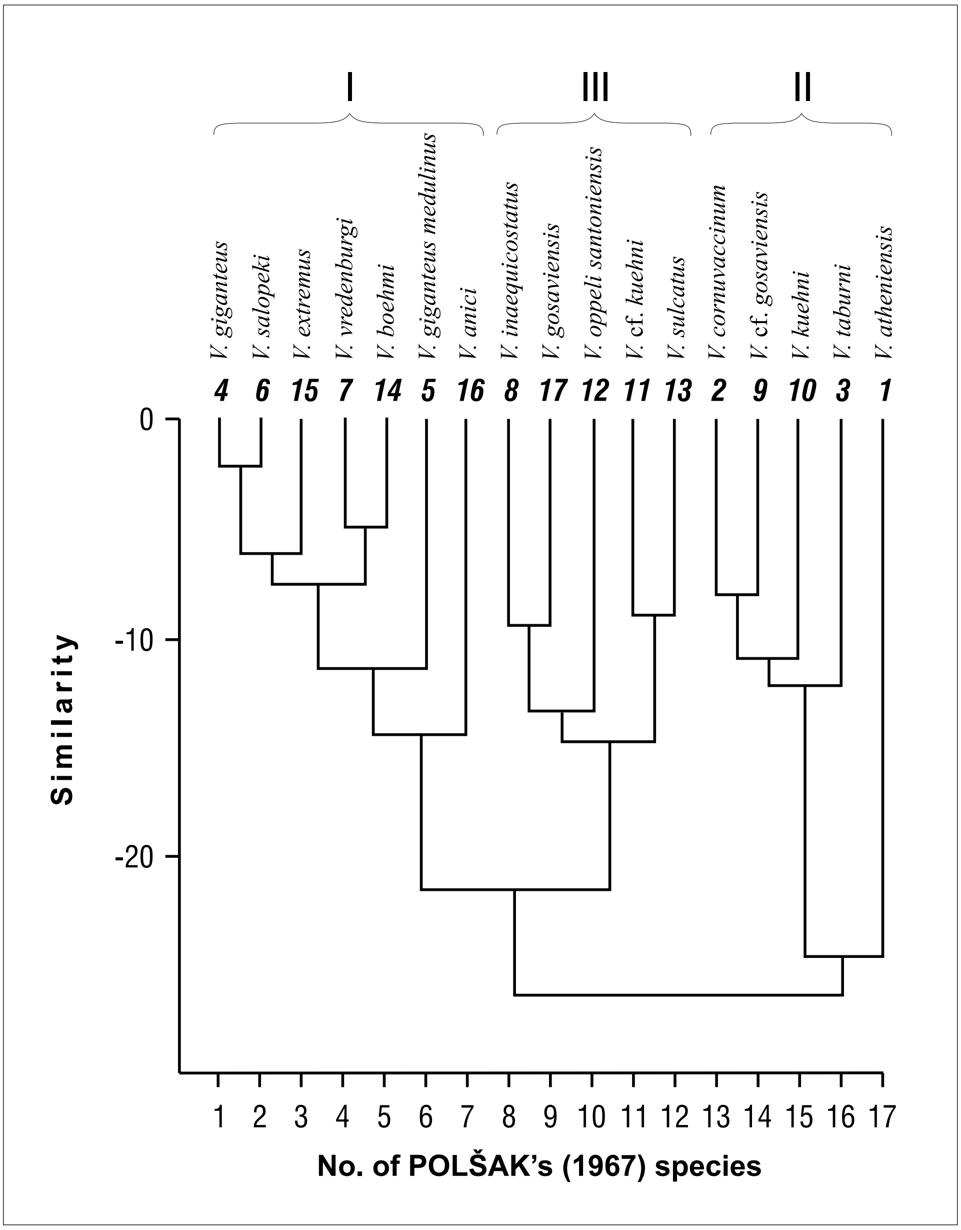

Fig. 4 Hierarchical cluster analysis (pair–group method) including all parameters for *Vaccinites* species from Santonian of southern Istria. Numbers I, II and III correspond to statistically determined groups.

close to each other. The teeth and their array are curved towards the anterior. A distinction between species included in this group, *V. vredenburgi* and *V. giganteus*, has been problematical for a while (LAVIANO & GUARNIERI, 1989; STEUBER, 1999).

The Group II (Fig. 2, Table 2) contain one of the oldest known hippuritid species, *Vaccinites cornuvaccinum* which is also the type species of the genus V*accinites* (BRONN, 1831; FISCHER, 1887; DECHASEAUX & COOGAN, 1969; STEUBER, 1999). Separating species, which are members of this group, *V. cornuivaccinum* from *V. taburni* has frequently been a problem, as well as another member of this group, *V. atheniensis*, which probably represents an adult growth stage of *V. chaperi* (STEUBER, 1999). Also, *V. cornuvaccinum* and *V. chaperi* are considered to be of the same stratigraphic age, as well as coenozone, on the Adriatic Carbonate Platform (SLIŠKOVIĆ, 1968; POLŠAK et al., 1982; STEUBER, 1999). The ligamental ridge is slightly curved toward the anterior, especially at the end. P_1 varies from parallel sided to considerably pinched at its base with an oval head. P_2 is pedunculated with an oval head which can be slightly curved in an anterior direction. P_1 and P_2 can be fused at their junction with the inner diameter of the shell. The teeth are almost in line with the ligament ridge.

Specimens of the Group III (Fig. 2, Table 2) are characterised by a straight ligamental ridge, slightly curved towards the anterior. P_1 has a round or oval head more or less pinched at its base and generally shorter than P_2. P_2 is straight, and pinched at the base with an elliptical head. Teeth are both beside and in prolongation of the ligamental ridge.

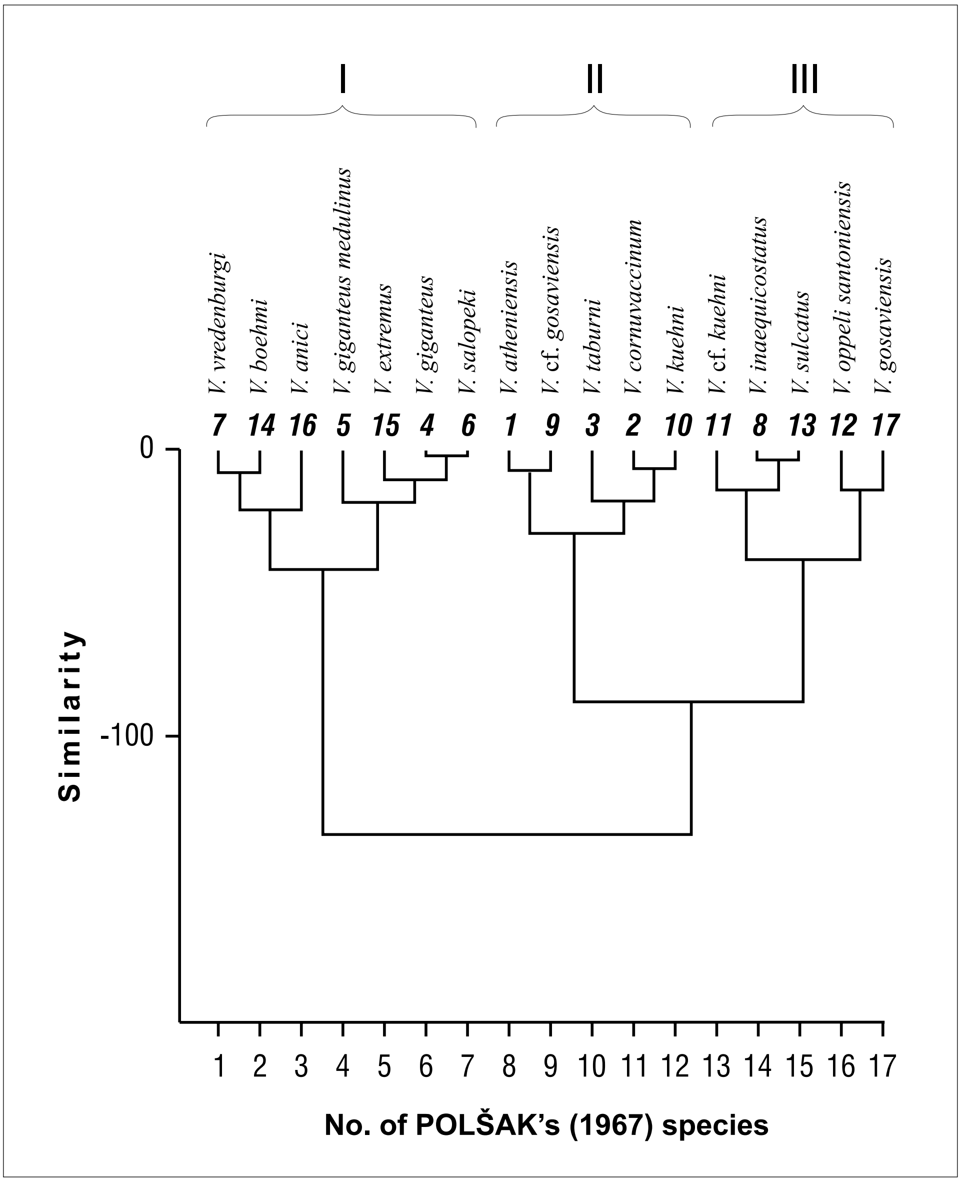

Fig. 5 Hierarchical cluster analysis (Ward's method) taking into account L/P_2 and L/T measurements for *Vaccinites* species (POLŠAK, 1965, 1967). Numbers I, II and III correspond to statistically determined groups.

5. CONCLUSION

The aim of this work has been to check the possibility of taxonomic re-evaluation of *Vaccinites* species using cluster analysis (Ward's and Unweighted pair-group average methods). Cluster analyses of the measured elements indicates a relationship between the position of the teeth, ligamental ridge, E pillar, the length of U contour and the P0–P2 suture distance in the Santonian *Vaccinites* species from southern Istria. The cluster analysis, based upon field and laboratory observations, results in the recognition of three groups.

The first group, *V. giganteus*, *V. giganteus medulinus*, *V. salopeki*, *V. vredenburgi*, *V. boehmi*, *V. extremus* and *V. anici*, shows angle values between 19 and 55º (L/ P_2), 42–74º (L/T), U values from 31–42.4 cm and U/P0–P2 from 6.3–10.6 cm. The dental array is curved in an anterior direction.

The second group includes the species *Vaccinites cornuvaccinum*, *V. chaperi* (=*V. atheniensis*), *V. taburni*, *V.* cf. *gosaviensis* and *V. kuehni*. The characteristics of this group are: L/P_2 values 2–27º, L/T values 7–20º, U values 24.2–84.6 cm and U/P0–P2 values 6.0–10 cm. The teeth are almost in the line with the ligament ridge.

The third group, *V. inaequicostatus*, *V.* cf. *kuehni*, *V. oppeli santoniensis*, *V. sulcatus* and *V. gosaviensis*, has angle values from 43 to 77º for L/P_2, 30º or less for L/T (between 15 and 30º), U values from 20.1– 46.5 cm, and U/P0–P2 from 5.1–7.1 cm. The teeth are beside and in prolongation of the ligamental ridge.

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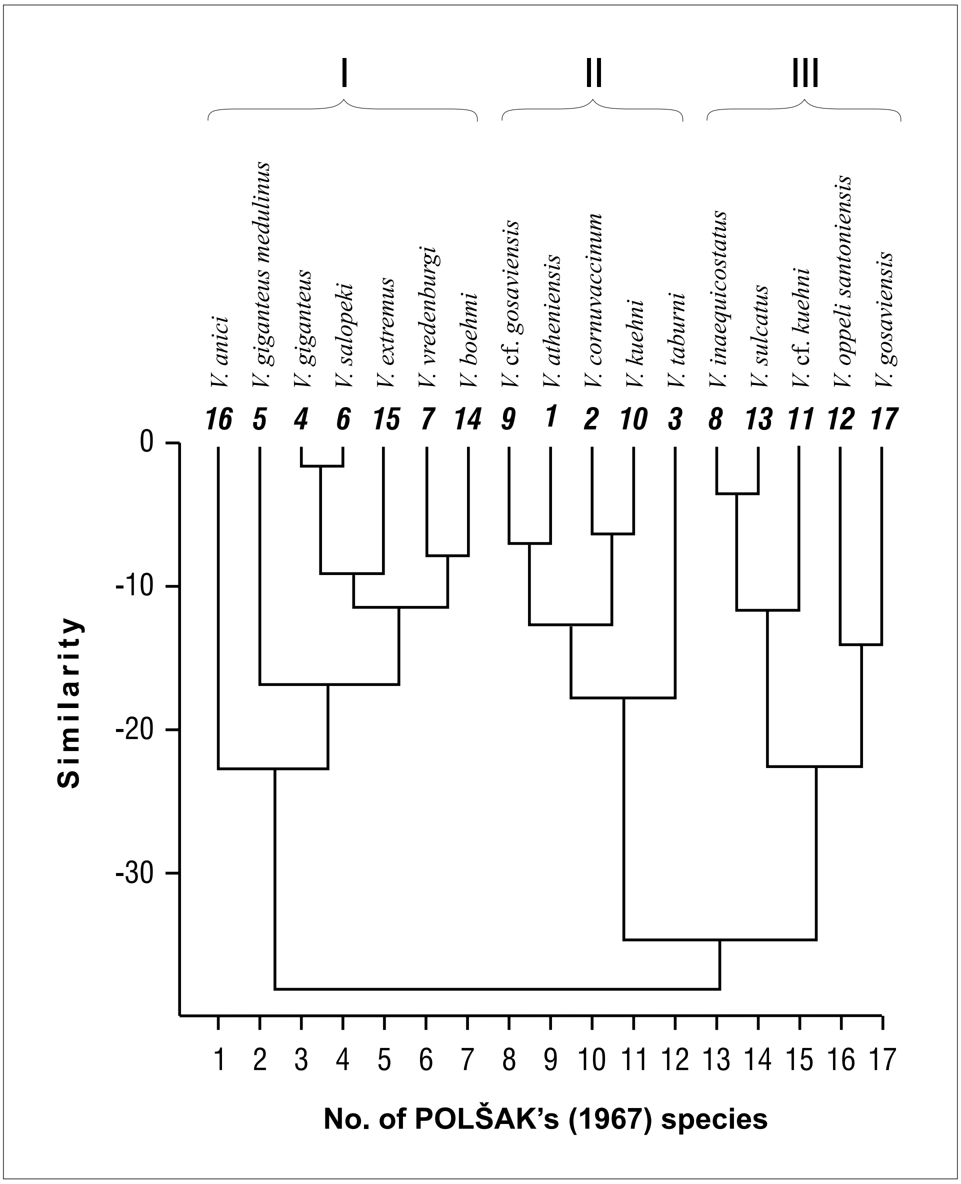

Fig. 6 Hierarchical cluster analysis (pair–group method) considering L/P$_2$ and L/T measurements for *Vaccinites* species (POLŠAK, 1965, 1967). Numbers I, II and III correspond to statistically determined groups.

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6. REFERENCES

BRONN, H.G. (1831): Hippurites.– In: ERSCH, J.S. & GRUBER, J.G. (eds.): Allgemeine Encyclopaedie der Wissenschaften und Künste. Brockhaus, Leipzig, 371–376.

DECHASEAUX, C. & COOGAN, A.H. (1969): Family Hippuritidae Gray, 1848.– In: MOORE, R.C. (ed.): Treatise on Invertebrate Paleontology. The Geological Society of America, University of Kansas, Lawrence, N799–N803.

FISCHER, P. (1887): Manuel de conchyliologie et de paléontologie conchyliologique ou historie naturelle des mollusques vivants et fossiles [*Guide for conchyology and conchyological palaeontology of recent and fossil molluscs of the natural history* – in French].– F. Savy, Paris, 1369 p.

HAMMER, O., HARPER, D.A.T. & RYAN, P.D. (2003): PAST–Paleontological statistics, Ver. 1.15.– http://folk.uio.no/ohammer/past.

LAVIANO, A. & GUARNIERI, G. (1989): *Vaccinites vredenburgi* KÜHN, 1932, from the Upper Cretaceous of Apulia (southern Italy).– Boll. Soc. Paleont. Ital., 28, 78–86.

LAVIANO, A. & MARESCA, M.G. (1992): Paleontological characters of the species *Vaccinites vesiculosus* (Woodward).– Geol. Romana, 28, 49–59.

MACLEOD, N. (2004): Prospectus and regression 1.– Palaeontological Newsletter. http://www.palass.org.

MORO, A. (1997): Stratigraphy, paleoecology and vertical succession of rudist biostromes in the Upper Cretaceous (Turonian–Santonian) limestones of southern Istria, Croatia.– Palaeo. Palaeo. Palaeo., 131, 113–131.

MORO, A. & ĆOSOVIĆ, V. (2000): The rudist assemblages of southern Istria – an example of environmentally induced succession within Santonian limestones.– Riv. Ital. Paleont. Strat., 106, 59–72.

PARKER, C.W. & ARNOLD, A.J. (1999): Quantitative methods of data analysis in foraminiferal ecology.– In: SEN GUPTA, B.K. (ed.): Modern Foraminifera. Kluwer Academic Publishers, Dorderecht, 71–89.

POLŠAK, A. (1965): Geologija južne Istre s osobitim obzirom na biostratigrafiju krednih naslaga (Géologie de l'Istrie méridionale spécialement par rapport a la biostratigraphie des couches Crétacées) [*The geology of southern Istria with special consideration of biostratigraphy of Cretaceous deposits* – in Croatian with French abstract].– Geol. vjesnik, 18, 415–509.

POLŠAK A. (1967): Kredna makrofauna južne Istre (Macrofaune Crétacée de l'Istrie méridionale, Yugoslavie) [*The Creaceous macrofauna of southern Istria* – in Croatian and French] – Palaeontologia jugoslavica, 8, 1–219.

POLŠAK, A., BAUER V. & SLIŠKOVIĆ T. (1982): Stratigraphie du Crétacé supérieur de la plate-forme carbonatée dans les Dinarides Externes [*Upper Cretaceous stratigraphy of the carbonate platform of the Outer Dinarides* – in French].– Cret. Res., 3, 125–133.

SIMONPIÉTRI, G. & PHILIP, J. (2000): Relations ontogenése-philogenése chez les rudistes: l'exemple des Hippuritidae Gray, 1848 [*Ontogeny–phylogeny relationships in rudists: the example of Hippuritidae Gray, 1848* – in French].– Sciences de la Terre et planétes, 330, 717–724.

SKELTON, P.W. (1976): Functional morphology of the Hippuritidae.– Lethaia, 9, 83–100.

SLIŠKOVIĆ, T. (1968): Biostratigrafija gornje krede južne Hercegovine [*Biostratigraphy of the Upper Cretaceous in Southern Herzegovina* – in Croatian].– Bulletin du Musée de la République Socialiste de Bosnie–Herzégovine á Sarajevo, Sciences Naturelles, Nouvelle Série, 7, 5–66.

STEUBER, T. (1999): Cretaceous rudists of Boeotia, central Greece.– Spec. Papers in Paleontology, 61, 229 p.

VICENS, E. (1992): Intraspecific variability in Hippuritidae in the Southern Pyrenees, Spain: Taxonomic implications.– Geol. Romana, 28, 119–161.

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