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On the presence of zygosphene-zygantrum vertebral articulations in salamandrids

[With 6 text-figs]

O występowaniu połączeń międzykręgowych typu zygosphene-zygantrum u *Salamandridae*

Abstract. The presence of zygosphene-zygantrum intervertebral articulations is documented for the first time in the order *Caudata*. In the newt *Salamandrina terdigitata* (*Salamandridae*) such articulation can be observed in both the trunk and caudal regions. Examination of the angular relations between the zygapophyseal and zygosphene articular surfaces allows quantification of the intracolumnar variation and makes possible its comparison with other amphibians and reptiles. The results indicate that the morphological degree of development of such articulation in *Salamandrina* approaches that of lacertilians. From an evolutionary point of view, this structure seems to have independently evolved in quite different lineages. Its functionality is here interpreted as related to an extreme concave bending of the columnar axis.

I. INTRODUCTION

The zygosphene-zygantrum intervertebral articulation consists anteriorly of two articular surfaces facing laterally on the walls of the cephalic part of the neural arch, and their corresponding structures on the posterior part of the previous vertebra. They make a type of tenon-mortise connection. These facets may or may not be in contact with the zygapophyseal ones. The presence of this type of articulation is known in *Sphenodon*, members of some lacertilian families (such as *Lacertidae*, *Teiidae* or *Cordylidae*) and all snakes (Hoffstetter and Gasc, 1969; Guibé, 1970). In the class *Amphibia* to my knowledge, this structure has not been recorded (e. g. Noble, 1955; Trueb, 1973; Duellman and Trueb, 1986), and only Sanchíz (1985; work in progress) has recently indicated its presence in the anuran *Bombina* (*Discoglossidae*).

The article documents the presence of a zygosphene-zygantrum articulation in a member of the order *Caudata*, the salamandrid newt *Salamandrina terdigitata* (Lacépède, 1788) and analyses its variation and degree of development in relation with snakes and lizards.

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II. MATERIALS AND METHODS

Dry skeletons (collection of the Museo Nacional de Ciencias Naturales, MNCN, Madrid, unless otherwise stated) of the following species have been measured: *Salamandridae*: *Salamandrina terdigitata* (MNCN 8306051-5, 8305191-4; province of Lucca, Italy). Samples of all other European salamandrid genera were also inspected for zygosphene-like structures, with negative results. *Discoglossidae*: *Bombina maxima* (Inst. Syst. Exper. Zool., Polish Acad. Sci., ZZSiD, Cracow), *Bombina orientalis* (MNCN 8412201-5, 8412207, 8412209-11, 8303101-2, 8211021-3). *Lacertidae*: *Lacerta lepida* (MNCN 8412224). *Teiidae*: *Tupinambis rufescens* (MNCN 8611201). *Colubridae*: *Malpolon monspessu-*

Table I

Angular intervertebral articulation measurements (Fig. 1) along a single vertebral column of *Salamandrina terdigitata*

Vertebrae	Alpha	Beta	Gamma	Vertebrae	Alpha	Beta	Gamma
V 2	85.0	71.0	24.0	V 23	89.0	76.0	15.0
V 3	94.0	64.0	21.5	V 24	102.5	73.0	4.5
V 4	97.5	72.0	10.5	V 25	107.0	66.0	7.0
V 5	112.0	69.5	1.5	V 26	109.5	63.5	7.0
V 6	89.0	87.0	4.0	V 27	109.0	71.0	0.0
V 7	110.0	68.5	1.5	V 28	113.5	67.5	−1.0
V 8	108.5	69.5	2.0	V 29	108.0	72.5	−0.5
V 9	111.0	67.5	1.5	V 30	117.5	66.5	−4.0
V 10	116.0	64.0	0.0	V 31	114.0	71.5	−5.5
V 13	103.0	72.0	5.0	V 32	124.0	71.5	−15.5
V 14	97.0	84.0	−1.0	V 33	120.5	77.5	−18.0
V 15	101.5	70.5	8.0	V 34	132.0	72.5	−24.5
V 16	97.0	75.0	8.0	V 35	135.5	62.0	−17.5
V 17	95.5	71.5	13.0	V 37	142.5	64.0	−26.5
V 18	99.0	69.0	12.0	V 38	148.0	52.5	−20.5
V 19	106.5	65.0	8.5	V 39	141.0	52.0	−13.0
V 20	99.0	64.5	16.5	V 40	143.0	43.0	−6.0
V 21	118.5	54.5	7.0	V 41	155.0	31.0	−6.0
V 22	96.5	67.5	16.0				

lanus (MNCN 8206021). With the exception of *Tupinambis rufescens*, which was hand prepared, all the material was skeletonized by natural maceration at 55—60°C and cleaned with approximately 3°/₀ H_2O_2.

Linear and angular measurements were taken by the use of enlarged camera lucida drawings. For each vertebra right and left measurements were taken and their mean used in the analyses. Repeated measuring of the same objects by different persons gave a variation on the order of 8 %. Triangular projections, based on the geometric propriety that for each point the sum of the perpendiculars to the three sides equals the triangle height (here set to 100), were done using a program devised by J. R. Elvira and L. García Cacho (MNCN, Madrid). In this case, taking into consideration the sign of the angular measurements (Fig. 1), the sum $\alpha + \beta + \gamma = 180°$.

Table II

Salamandrina terdigitata. Statistics of vertebral angular measurements (Fig. 1). N — sample size, S. D. — standard deviation

Vertebrae	N	Alpha		Beta		Gamma	
		Mean	S. D.	Mean	S. D.	Mean	S. D.
V 2	7	86.07	14.37	75.43	13.03	17.79	6.33
V 3	9	102.17	11.78	69.61	8.33	8.22	7.40
V 6	9	110.83	13.70	67.78	12.75	1.39	2.76
V 8	9	107.94	11.21	69.33	10.71	2.67	3.95
V 10	8	111.13	9.16	67.19	7.42	1.69	3.54
V 12	8	107.31	9.35	69.31	7.17	3.37	5.20
Sacrum	9	108.22	16.57	68.56	12.10	3.22	6.66

Table III

Statistics of angular measurements on trunk vertebrae in *Anura*, *Sauria* and *Serpentes*. N — sample size, S. D. — standard deviation

Taxa	N	Alpha		Beta		Gamma	
		Mean	S. D.	Mean	S. D.	Mean	S. D.
Bombina orientalis V_4	14	130.21	10.768	57.86	8.084	−8.07	5.223
V_5	14	131.80	10.910	53.00	7.279	−4.80	5.896
V_6	14	126.25	11.967	59.59	10.797	−6.30	4.960
V_7	14	125.29	9.480	56.45	7.983	−1.73	9.245
Lacerta lepida	6	89.13	4.593	62.75	3.847	28.13	2.489
Tupinambis rufescens	9	47.81	7.599	105.86	8.086	26.33	1.000
Malpolon monspessulanus	7	55.68	3.475	122.36	1.567	1.96	2.205

Table IV

Salamandrina terdigitata. Linear measurements of the segments AA', AB, BC and CC' (defined in Fig. 1), in selected vertebrae (V), in mm. N — sample size, S. D. — standard deviation

V	N	AA'		AB		BC		%BC		CC'	
		Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.	Mean	S. D.
V 2	8	1.16	0.081	0.35	0.074	0.17	0.021	50.8	11.14	0.47	0.061
V 3	9	1.26	0.053	0.35	0.035	0.17	0.028	47.2	10.27	0.47	0.051
V 6	9	1.57	0.088	0.49	0.044	0.19	0.035	39.4	7.85	0.47	0.033
V 8	9	1.59	0.069	0.51	0.025	0.19	0.024	36.8	4.91	0.46	0.031
V 10	9	1.65	0.071	0.53	0.026	0.18	0.024	33.9	5.41	0.45	0.034
V 12	9	1.70	0.083	0.55	0.035	0.19	0.029	35.2	6.12	0.49	0.043
V s	9	1.76	0.101	0.54	0.038	0.18	0.027	33.4	6.15	0.57	0.070

III. DESCRIPTION

The presence of a zygosphene-zygantrum articulation, in *Salamandrina terdigitata*, with a qualitatively similar degree of development to that of *Sphenodon* (Hoffstetter and Gasc, 1969), can be observed in practically all the regions of the

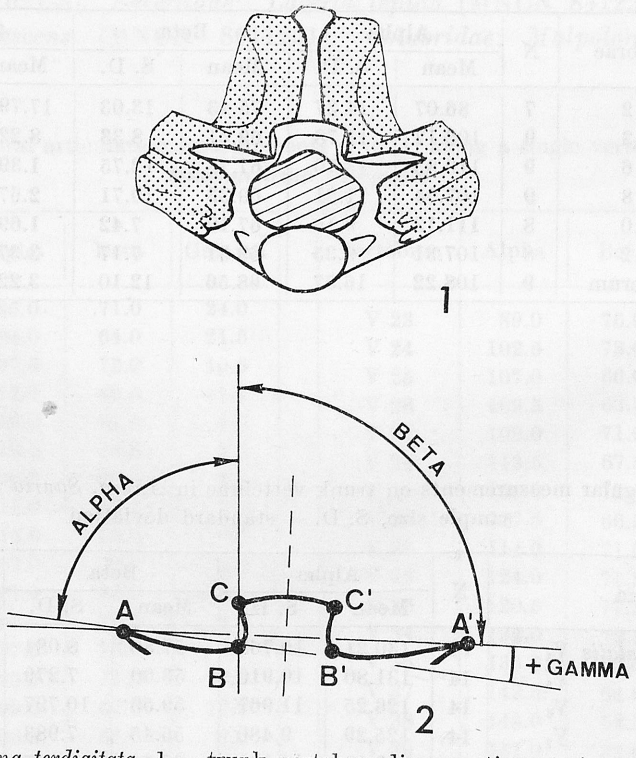

Fig. 1. *Salamandrina terdigitata.* 1 — trunk vertebra, diagramatic anterior view, 2 — zygosphene-zygapophyseal complex with right angular measurements. Alpha — vertex on B, Beta — vertex on the intersect AA'-BC, Gamma — vertex on A, positive if below AA', negative above AA'; B is the most extreme point from the axis AC on the zygosphene-zygapophyseal anterior margin

column of this small newt (Fig. 1 and 2). The zygosphenic and zygantral facets are in contact with the zygapophyseal ones, and they form an angle about 110° for most of the trunk and caudal regions. There is no anterior dorsal notch on the neural arch. Jointly with zygapophyses and the peculiar neurapophyses and neural plate that this genus possesses, they indicate a high degree of vertebral imbrication.

Tables I and II give respectively the angular measurements (Fig. 1) at all the positions in a single column (Fig. 3) and on several individuals for se-

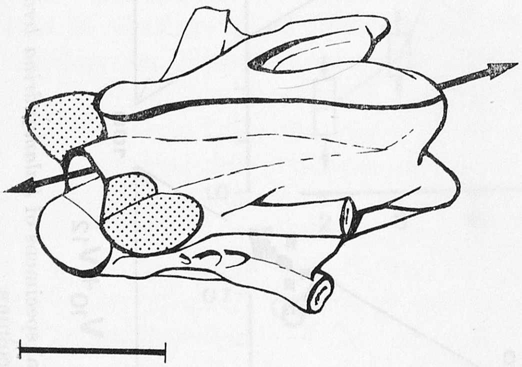

Fig. 2. *Salamandrina terdigitata*. Diagramatic middle trunk vertebra (V_8), anterior-lateral upper view. Scale equals 1 mm

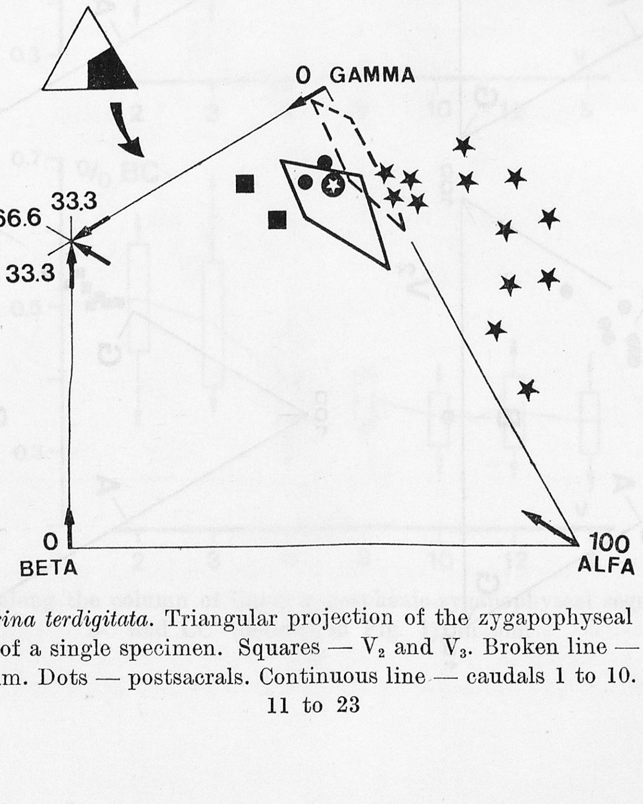

Fig. 3. *Salamandrina terdigitata*. Triangular projection of the zygapophyseal angles along the vertebral column of a single specimen. Squares — V_2 and V_3. Broken line — V_4 to V_{14}. Circle with star — sacrum. Dots — postsacrals. Continuous line — caudals 1 to 10. Stars — caudals 11 to 23

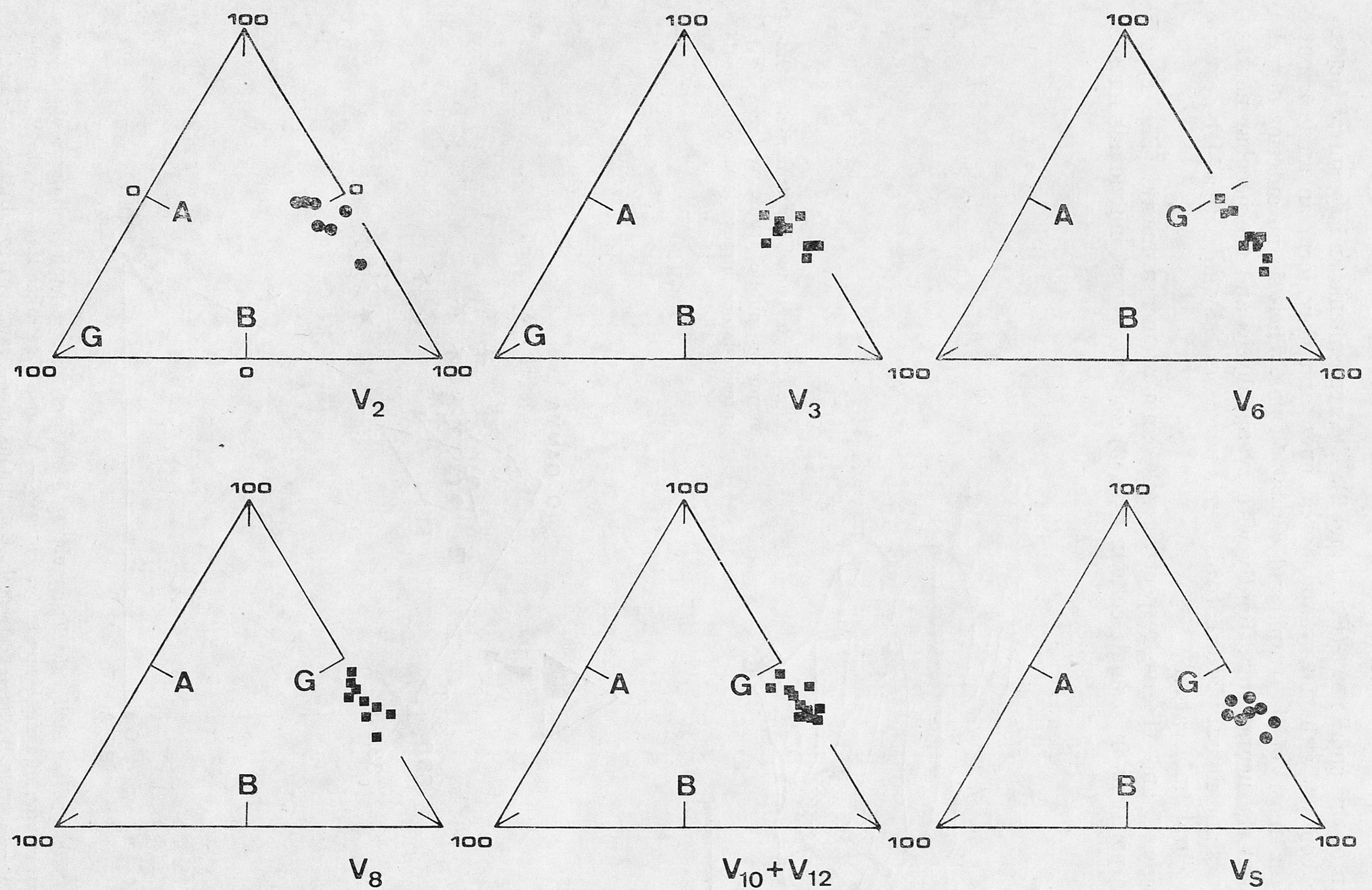

Fig. 4. Triangular projection of the zygapophyseal angles of several specimens of *Salamandrina terdigitata* at different levels of the vertebral column

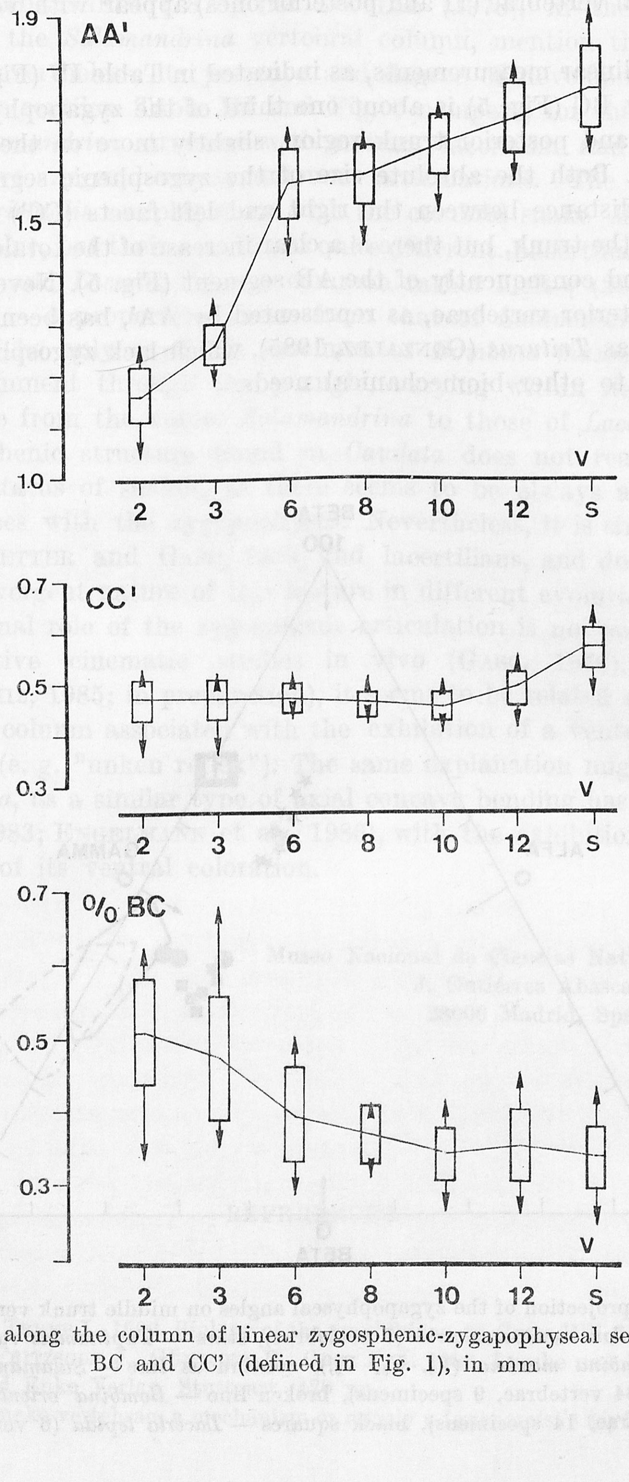

Fig. 5. Variation along the column of linear zygosphenic-zygapophyseal segments AA', AB, BC and CC' (defined in Fig. 1), in mm

lected vertebrae (Fig. 4). A regionalization seems clear with the joint use of the three angles, because groups including V_2+V_3, trunk, sacrum to caudal 10, anddistal caudal vertebrae (11 and posterior ones) appear with very little overlapping.

Concerning linear measurements, as indicated in Table IV (Fig. 1), the zygosphene segment BC (Fig. 5) is about one third of the zygapophyseal one (AB) on the middle and posterior trunk region, slightly more on the most anterior columnar level. Both the absolute size of the zygosphenic segment (BC) and the minimum distance between the right and left facets (CC') remain almost constant along the trunk, but there is a clear increase of the total zygapophyseal width (AA'), and consequently of the AB segment (Fig. 5). Nevertheless, widening of the posterior vertebrae, as represented by AA', has been found in salamandrids such as *Triturus* (GONZALEZ, 1985), which lack zygosphenes, and probably respond to other biomechanical needs.

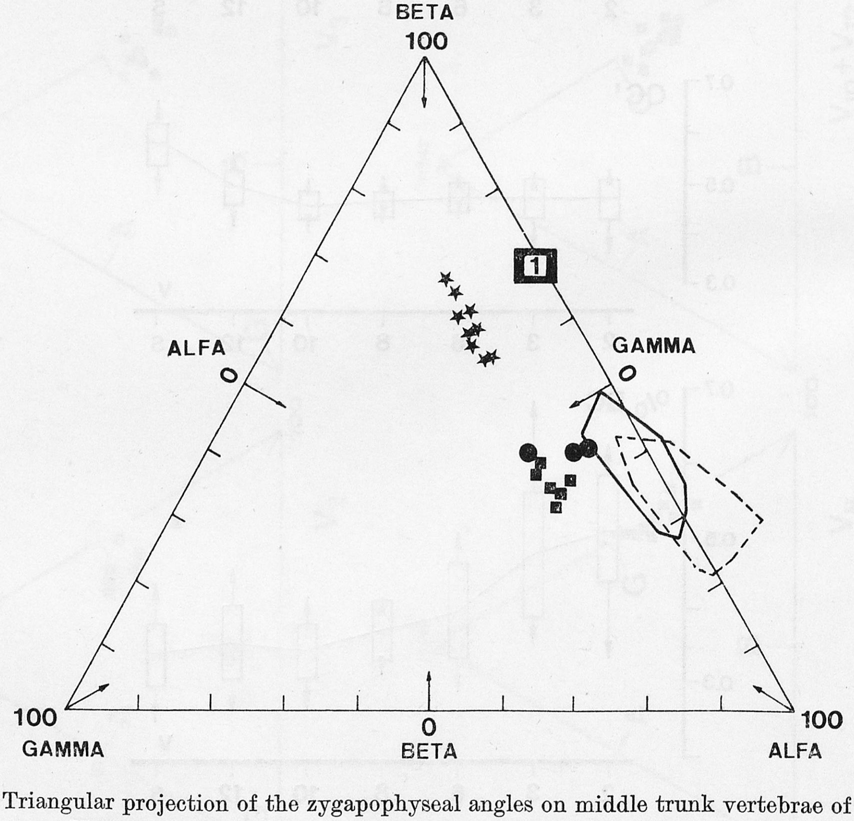

Fig. 6. Triangular projection of the zygapophyseal angles on middle trunk vertebrae of several groups. 1 — *Malpolon monspessulanus* (7 vertebrae), stars — *Tupinambis rufescens* (9 vertebrae), dots — *Bombina maxima* (V_4, V_5, V_6,), continuous line — *Salamandrina terdigitata* (V_6, V_8, V_{10}, V_{12}, 34 vertebrae, 9 specimens), broken line — *Bombina orientalis* (V_4, V_5, V_6; 42 vertebrae, 14 specimens), black squares — *Lacerta lepida* (6 vertebrae)

IV. DISCUSSION

Neither WIEDERSHEIM (1875) nor NAYLOR (1978), in their osteological descriptions of the *Salamandrina* vertebral column, mention the zygosphenic articulation. Nevertheless, its presence and degree of development is similar to that of some reptiles. Table III and Fig. 6 compare, for the middle trunk region, the *Salamandrina* structure with anuran, lacertilian and snake species known to have zygosphenic-zygantrum articulations. The *Salamandrina* and *Bombina orientalis* samples share with the colubrid snake *Malpolon* a very low γ angular value, but their α and β are quite different. Lacertilians, represented by *Tupinambis* and *Lacerta*, share a common rather high γ (26—28°), but he range of their α—β proportion varies from that of *Salamandrina* up to the ophidian one. The only available specimen of *Bombina maxima* breaks this pattern of alignment through the γ angle, varying within its three middle trunk vertebrae from the values *Salamandrina* to those of *Lacerta*.

The zygosphenic structure found in *Caudata* does not reach the highly differentiated status of snakes, as there seems to be always a continuity of articular surfaces with the zygapophyses. Nevertheless, it is similar to *Sphenodon* (HOFFSTETTER and GASC, 1969) and lacertilians, and documents quite clearly the convergent nature of this feature in different evolutionary lineages.

The functional role of the zygosphenic articulation is not well understood, lacking definitive cinematic studies in vivo (GASC, 1976). At least in anurans (SANCHIZ, 1985; in preparation), it seems to be related with a concave bending of the column associated with the exhibition of a ventral aposematic colour pattern (e. g. "unken reflex"). The same explanation might be the case of *Salamandrina*, as a similar type of axial concave bending has been reported (e. g. LANZA, 1983; ENGELMANN et al., 1986), with the exhibition of the black and red parts of its ventral coloration.

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STRESZCZENIE

W niniejszej pracy po raz pierwszy udokumentowano występowanie połączeń międzykręgowych typu zygosphene-zygantrum w obrębie rzędu płazów ogoniastych (*Caudata*). Połączenia stawowe tego typu występują zarówno w części tułowiowej, jak i ogonowej kręgosłupa u *Salamandrina terdigitata* (*Salamandridae*). Badania zależności kątowych pomiędzy powierzchniami stawowymi zygosphene i wyrostków stawowych (zygapophyses) pozwalają na ilościowe określenie zmienności w obrębie kręgosłupa oraz umożliwiają jej porównanie z innymi płazami i gadami. Uzyskane wyniki wskazują, że stopień morfologicznego rozwoju tych połączeń u *Salamandrina* jest podobny jak u jaszczurek. Z ewolucyjnego punktu widzenia rozwój tych struktur nastąpił niezależnie w obrębie różnych grup systematycznych. Obecność tych połączeń stawowych wiąże się ze zdolnością do znacznego wyginania kręgosłupa w płaszczyźnie pionowej.

RESUMEN

Se pone de manifiesto por primera vez la presencia de articulaciones intervertebrales del tipo zigosfeno-zigantro en el orden *Caudata*. En *Salamandrina terdigitata* (*Salamandridae*) puede observarse esa articulación tanto en la región troncal como caudal. Un examen de las relaciones angulares existentes entre las facetas articulares de zigapófisis y zigosfeno permite la cuantificación de la variación intracolumnar y posibilita su comparación con otros anfibios y reptiles. Los resultados indican que el grado de desarrollo de esa articulación en *Salamandrina* se acerca al de los *Sauria*. Desde una perspectiva evolutiva, esta estructura parece haberse desarrollado de manera independiente en linajes muy alejados entre sí. Su función se interpreta en este trabajo como relacionada con el curvamiento cóncavo del eje columnar.

Edited by Dr. Z. Szyndlar