

Supplementary Data

A new exceptionally preserved specimen of *Dracaenosaurus* (Squamata, Lacertidae) from the Oligocene of France as revealed by micro-computed tomography

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APPENDIX 1S. Codings for taxa added to the matrix of Čerňanský et al. (2016).

*Dracaenosaurus croizeti*

200110211111100?00??1012110000101101010041?????2??????????????

*Timon lepidus*

2010103111010110100100120001011(01)1101101121100(01)000001102110010100

*Acanthodactylus erythrurus*

0?211021111001120010001222010122000010012112011311?1104120??1000

*Podarcis hispanica*

01022011111001000010001202001211110?100010?200(01)3000000(01)001111000

*Psammodromus hispanicus*

0012202011001201001110111100020111000101102000030121114000020011

APPENDIX 2S. Changes to codings in the original matrix of Čerňanský et al. (2016).

*Pseudeumeces cadurcensis* 2:0 →?, 13:? →1, 28:? →0

*Psammodromus algirus* 4:2 →1, 5:0 →2, 42:3 →2

*Gallotia galloti*: 4:1 →2, 5:0 →2, 42:3 →2

*Gallotia stehlini*: 4:1 →2, 5:0 →1, 42:3 →2

*Lacerta agilis*: 19: ? →0

APPENDIX 3S. List of characters of Čerňanský et al. (2016).

1. Size of the skull: (0) less than 20 mm; (1) 20 to 40; (3) more than 40 mm. ORDERED.
2. Skull: (0) tall; (1) depressed (Arnold, 1989).
3. Medial depression of the snout: (0) absent; (1) weak; (2) strong. ORDERED.
4. Nasal process of premaxilla: (0) broad; (1) intermediate; (2) slender (sensu Arnold et al., 2007).ORDERED.
5. Angle of the nasal process of premaxilla to the horizontal plane: (0) around 80°; (1) around 60°; (2) around 40°. ORDERED. Please note that we have considered that it is sometimes difficult to provide an accurate coding for this character, and we have excluded it from the current analyses. It was not completely deleted because we wanted to keep the same correlation between numbers and characters as in the original matrix of Čerňanský et al (2016), and because this character might be useful in future versions of the matrix.
6. Size of maxillary process of premaxilla: (0) normal size, (1) reduced.
7. Premaxillary tooth count in adults: (0) one to three; (1) four to six; (2) seven to eight ; (3) 9 or more. ORDERED.
8. Premaxillary teeth size (apart from median tooth): (0) similar in size to or larger than anterior maxillary teeth, (1) distinctly smaller than anterior maxillary teeth.
9. Maxilla-frontal contact: (0) absent, (1) present (2).
10. Maxilla is excluded from orbit: (0) absent, (1) present.
11. Maxilla-jugal contact: (0) smooth; (1) stepped (Arnold, 1989).
12. Maxilla posterior process, posterior extent: (0) reaches mid-orbit; (1) posterior to mid-orbit (Lee and Scanlon, 2002).
13. Maxillary tooth crown size and height: (0) constant throughout tooth row, (1) increases posteriorly (Gauthier et al., 2012).
14. Maxillary tooth count: (0) 16 or fewer; (1) 17 to 19; (2) 20 to 25; (3) more than 25. ORDERED.
15. Pterygoid teeth: (0) absent; (1) present.

16. Septomaxilla: (0) simply convex above with rounded posterior margin and narrow anterior shelf with at most slight anterior and posterior projection; (1) with distinct and widely separated anterior and posterior projections; (2) with distinct and widely separated anterior and posterior projections and a clear posterolateral process; (3) with distinct posterior and posterolateral projections but no anterior projection; (4) with distinct posterior projection and posterolateral process, no anterior projection but an anterolateral process (Arnold, 1989).
17. Nasal length relative to frontal length: (0) nasals very short, about one-third of frontal length, (1) nasals short, about one-half of frontal length; (2) nasals longer than frontals. ORDERED.
18. Nasal-prefrontal contact: (0) absent; (1) present (Gauthier, 1982).
19. Postnasal scales: (0) two superposed; (1) single (Arnold, 1989).
20. Postfrontal and postorbital in juveniles: (0) separated; (1) fused (Arnold, 1973).
21. Posteroventral process of jugal: (0) strong; (1) weak (Arnold, 1989).
22. Position of medial ridge on the internal side of jugal: (0) Type 1; (1) Type 2 (Čerňanský et al., 2014).
23. Jugal lateral exposure below orbit: (0) absent; (1) partly exposed above orbital margin of maxilla; (2) distinct part exposed above orbital margin of maxilla (Estes et al., 1988). ORDERED.
24. Ratio of posterior and anterior portion between the sulcus interfascialis on frontal: (0) 1:1; (1) 3:4; (2) 1:2 to 1:3 (sensu Čerňanský, 2010). ORDERED.
25. Frontals: (0) discrete; (1) partially fuse in later ontogeny; (2) fused (Estes et al., 1988; Arnold, 1989).
26. Interorbital constriction of the frontal: (0) usually absent; (1) usually present; (2) strong. ORDERED.
27. Subolfactory process of the frontal: (0) reaching palatines and in continuous contact with prefrontal, so anterior surface of the orbit is completely bony; (1) not descending fully or a window present between each process and the adjoining prefrontal bone; (2) process absent (Arnold, 1989; Pregill et al., 1986). ORDERED.
28. Supratemporal processes of parietal: (0) long; (1) short
29. Sulcus medialis formed by cristae cranii parietalis: (0) present; (1) absent.
30. Interparietal scute: (0) short; (1) more or less the same anteroposterior length as portion of occipital scute on osteodermal crust; (2) large, longer than occipital scute. ORDERED.
31. Occipital scute: (0) anteroposteriorly short, shorter than interparietal scute; (1) long, trapezoidal; (2) absent
32. Occipital scute: (0) wider than interparietal; (1) equal; (2) narrower. ORDERED.
33. Parietal table: (0) square; (1) elongate.
34. Parietal coverage of braincase in dorsal view: (0) occiput broadly exposed; (1) occiput significantly covered; (2) occiput fully covered, or nearly so (Estes et al., 1988). ORDERED.
35. Parietal posterior margin near midline: (0) broadly concave or straight; (1) with paired processes; (2) parietal notch is present.
36. Ossification of temporal scales: (0) not extensive; (1) extensive.
37. Dentary length: (0) equals rest of jaw; (1) longer.
38. Dorsal curvature of the subdental shelf in the symphyseal region: (0) strong; (1) weak.
39. Dentary angular process: (0) angular process extends to or past coronoid apex, (1) anterior to coronoid apex, (2) anterior to level of coronoid bone (Gauthier, 1982). ORDERED.
40. The dentary tooth number: (0) 19 or fewer; (1) 20 to 24; (2) 25 or more. ORDERED.

41. Teeth: (0) with labial and lingual cusp; (1) bicuspid (mesial and distal); (2) tricuspid; (3) polycuspid, i.e., more than 3; (4) amblyodont.
42. Angle between the anteromedial and posteriomedial processes of coronoid in medial aspect: (0) more open; (1) more narrow.
43. Clavicle: (0) without loop; (1) interrupted loop; (2) complete loop.
44. Sternal fontanelle: (0) large and roughly elliptical; (1) sometimes very weakly heart-shaped; (2) clearly heart-shaped in at least some individuals; (3) small and round, or absent (Arnold, 1989).
45. Marked sexual variation in number of presacral vertebrae (0) yes; (1) no (Arnold, 1989).
46. Number of short free dorsal ribs: (0) equal or less than number of long free dorsal ribs; (1) more than number of long free dorsal ribs (Arnold, 1989).
47. Inscriptional ribs: (0) often present; (1) absent (Arnold, 1989).
48. Transverse processes on anterior autotomic caudal vertebrae: (0) in some individuals a long anterior pair of processes more or less at right angles to vertebra and a shorter parallel posterior pair; (1) only anterior pair present in all individuals; (2) a long anterior pair and a posterior pair that diverge posteriorly, posterior pair may be rather longer; (3) divergent anterior and posterior pairs, posterior pair always longer (Arnold, 1989).
49. Position of lateral border of parietal scute relative to parietal table of the skull: (0) not reaching edge of table; (1) reaching the edge of table posteriorly; (2) reaching edge of table anteriorly as well (Arnold, 1989). ORDERED.
50. Messenteric scale: (0) present in at least some individuals; (1) always absent (Arnold, 1989).
51. Collar beneath throat: (0) well developed, with granules beneath; (1) well developed, without granules beneath and fixed at centre; (2) collar weak; (3) absent (Arnold, 1989).
52. Number of longitudinal rows of ventral body scales (0) usually six; (1) usually eight; (2) usually ten or more (Arnold, 1989). ORDERED.
53. Blue pigmentation on outer ventral scales: (0) present; (1) absent (Arnold, 1989).
54. Tongue colour: (0) predominantly dark; (1) predominantly light (Arnold, 1989).
55. Nasal vestibule: (0) short; (1) some elongation; (2) vestibule overhangs posteriorly; (3) septomaxilla largely covered by vestibular overhang; (4) vestibular overhang covers anterior part of concha where it attaches to lateral wall of nasal cavity (Arnold, 1989).
56. Insertation of m. retractor lateralis anterior in front of vent: (0) near midline; (1) more laterally (Arnold, 1984).
57. Thoracic fascia: (0) none; (1) lateral; (2) expanding to mid-line (Arnold, 1989). ORDERED.
58. Length of hemipenial lobes: (0) relatively short; (1) relatively long (Arnold, 1989).
59. Lips on hemipenial lobes: (0) moderate or quite small; (1) large (Arnold, 1989).
60. Hemipenial microornamentation: (0) crown-shaped tubercles; (1) bicuspid tubercles; (2) simple spines (Arnold, 1989).
61. Exit to oviducts into genital sinus: (0) ventrally some way from tip(s) of sinus; (1) at or near the tip dorsally (Arnold, 1989).
62. Lateral septum on bodenaponeurois: (0) present; (1) absent (Arnold, 1989).
63. Voice: (0) usually mute; (1) squeak frequently (Böhme et al., 1985).
64. Copulatory position: (0) male grasps female by flank; (1) male grasps female by neck or mid-back (Arnold, 1989).

# APPENDIX 4S. Apomorphy lists (see Fig. 1S for the position of nodes).

Branch	Character	Steps	CI	Change
<i>Smaug giganteus</i> <-> node_19				
	1 (size of skull)	1	0.333	2 <-> 0
	2 (Skull)	1	0.500	1 <-> 0
	6 (Premaxillary maxilar process)	1	0.500	1 <=> 0
	8 (premaxillary teeth)	1	1.000	0 <=> 1
	9 (maxilla frontal contact)	1	1.000	0 <=> 1
	10 (Maxilla is excluded from orbit)	1	1.000	0 <=> 1
	15 (Pterygoid dentition)	1	0.333	0 <-> 1
	17 (nasal length relative to frontal length)	1	1.000	1 <=> 0
	18 (nasal - prefrontal contact)	1	1.000	1 <=> 0
	22 (The position of the medial ridge)	1	1.000	1 <=> 0
	23 (Jugal exposure below orbit)	1	1.000	0 <=> 1
	25 (frontals)	1	0.500	2 <=> 0
	27 (Subolfactory process of frontals)	1	1.000	1 <=> 0
	28 (Parietal supratemporal processes)	1	0.500	1 <-> 0
	31 (Occipital scute)	1	0.500	2 <-> 0
	34 (Parietal extends over braincase in dorsal view)	1	0.500	2 <=> 1
	35 (Parietal posterior mid-region)	1	1.000	1 <=> 0
	41 (teeth)	1	0.800	0 <=> 1
	42 (The angle between coronoid anterior and posterior process)	1	0.333	1 <-> 0
	43 (Clavicle)	1	1.000	0 <-> 1
	44 (sternal fontanelle)	1	1.000	3 <=> 0
	47 (Inscitional ribs)	1	1.000	1 <=> 0
	48 (transverse processes on autotomic caudal vertebrae)	1	1.000	1 <=> 2
node_19 --> node_20				
	4 (Nasal process of premaxilla)	1	1.000	0 ==> 1
	13 (Maxillary tooth size)	1	1.000	0 ==> 1
	16 (Septomaxilla)	1	1.000	0 ==> 1
	21 (posteroventral process of jugal)	1	1.000	0 ==> 1
	37 (dentary length)	1	1.000	1 ==> 0
	38 (The elevation of the anterior dentary region bearing symphysis)	1	1.000	0 ==> 1
	43 (Clavicle)	1	1.000	1 --> 2
	52 (number of longitudinal rows of ventral body scales)	1	1.000	0 --> 2
	54 (Tongue colour)	1	1.000	0 ==> 1
	55 (nasal vestibule)	1	1.000	2 --> 4
	63 (voice)	1	1.000	0 --> 1
	64 (copulatory position)	1	1.000	0 ==> 1
node_20 --> node_21				
	1 (size of skull)	1	0.333	0 --> 1
	14 (Maxillary tooth count)	1	0.500	2 ==> 0
	25 (frontals)	1	0.500	0 ==> 1
	40 (dentary tooth number)	1	0.667	1 ==> 0
	41 (teeth)	1	0.800	1 ==> 4
	45 (Marked sexual variation in presacral vertebra)	1	1.000	0 --> 1
	53 (blue pigmentation on outer ventral scales)	1	0.333	1 --> 0
node_21 --> node_22				
	1 (size of skull)	1	0.333	1 --> 2
	30 (Interparietal)	1	1.000	2 ==> 0
	31 (Occipital scute)	1	0.500	0 --> 1
	32 (occipital scute)	1	0.667	1 ==> 0
node_22 --> node_24				
	24 (The ratio of anterior and posterior frontal region)	1	0.667	2 ==> 1
	34 (Parietal extends over braincase in dorsal view)	1	0.500	1 --> 2
	39 (dentary angular process reduced)	1	0.500	0 ==> 1
node_24 --> node_23				

4 (Nasal process of premaxilla)	1	1.000	1 ==> 2
6 (Premaxillary maxilar process)	1	0.500	0 ==> 1
11 (maxilla - jugal contact)	1	0.500	1 ==> 0
41 (teeth)	1	0.800	4 --> 2
node_23 --> <i>Gallotia galloti</i>			
1 (size of skull)	1	0.333	2 ==> 1
node_23 --> <i>Gallotia stehlini</i>			
14 (Maxillary tooth count)	1	0.500	0 ==> 2
25 (frontals)	1	0.500	1 ==> 0
26 (mediolateral constriction of frontals)	1	0.500	1 ==> 0
40 (dentary tooth number)	1	0.667	0 ==> 1
41 (teeth)	1	0.800	2 --> 3
node_22 --> <i>Dracaenosaurus croizeti</i>			
15 (Pterygoid dentition)	1	0.333	1 --> 0
42 (The angle between coronoid anterior and posterior process)	1	0.333	0 ==> 1
node_20 --> <i>Psammodromus algirus</i>			
7 (Premaxillary teeth in adults)	1	0.500	2 ==> 3
11 (maxilla - jugal contact)	1	0.500	1 ==> 0
24 (The ratio of anterior and posterior frontal region)	1	0.667	2 ==> 1
51 (collar beneath trough)	1	1.000	0 ==> 3
59 (lips on hemipenial lobes)	1	0.500	0 --> 1
61 (exit to oviduct into genital sinus)	1	0.500	0 --> 1
node_19 --> node_18			
14 (Maxillary tooth count)	1	0.500	2 ==> 1
20 (Postfrontal and postorbitofrontal)	1	1.000	1 ==> 0
31 (Occipital scute)	1	0.500	0 --> 1
50 (Messeritic scale)	1	1.000	1 ==> 0
node_18 --> node_17			
1 (size of skull)	1	0.333	0 --> 1
3 (Medial depression of snouth)	1	0.500	0 --> 1
12 (Maxilla posterior process)	1	1.000	1 ==> 0
19 (postnasal scute)	1	1.000	1 ==> 0
28 (Parietal supratemporal processes)	1	0.500	0 --> 1
32 (occipital scute)	1	0.667	1 --> 0
42 (The angle between coronoid anterior and posterior process)	1	0.333	0 --> 1
48 (transverse processes on autotomic caudal vertebrae)	1	1.000	2 ==> 0
49 (position lateral border of parietal scute relative to parietal table of skull)	1	1.000	2 ==> 0
56 (insertation of m. retractor lateralis anterior in front of vent)	1	1.000	0 ==> 1
58 (length of hemipenial lobes)	1	1.000	1 ==> 0
node_17 --> node_16			
7 (Premaxillary teeth in adults)	1	0.500	2 ==> 3
26 (mediolateral constriction of frontals)	1	0.500	1 ==> 0
31 (Occipital scute)	1	0.500	1 --> 0
32 (occipital scute)	1	0.667	0 --> 2
55 (nasal vestibule)	1	1.000	2 ==> 0
node_16 --> <i>Lacerta viridis</i>			
14 (Maxillary tooth count)	1	0.500	1 ==> 2
25 (frontals)	1	0.500	0 ==> 1
53 (blue pigmentation on outer ventral scales)	1	0.333	1 ==> 0
node_16 --> <i>Lacerta agilis</i>			
1 (size of skull)	1	0.333	1 --> 0
3 (Medial depression of snouth)	1	0.500	1 --> 0
33 (The parietal table)	1	1.000	1 ==> 0
41 (teeth)	1	0.800	1 ==> 2
node_17 --> <i>Timon pater</i>			

FIGURE 1S. Bootstrap majority-rule consensus tree obtained in the first analysis with characters unordered and equally weighted. Numbers correspond to nodes in list of apomorphies (Appendix 4S).

## LITERATURE CITED

- Arnold, E. N. 1973. Relationship of the Palaearctic lizards assigned to genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). Bulletin of the British Museum (Natural History, Zoology) 25:291–366.
- Arnold, E. N. 1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. Symposia of the Zoological Society London 52:47–85.
- Arnold, E. N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an old-world family of lizards derived from morphology. Bulletin of the British Museum, Natural History, Zoology 55:209–257.
- Arnold, E. N., O. Arribas, and S. Carranza. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa 1430:1–86.
- Böhme, W., R. Hutterer, and W. Bings. 1985. Die Stimme der Lacertidae, speziell der Kanareneidechsen (Reptilia: Sauria). Bonner Zoologische Beiträge 36:337–354.
- Čerňanský, A. 2010. Earliest world record of green lizards (Lacertilia, Lacertidae) from the Lower Miocene of Central Europe. Biologia 65:737–741.
- Čerňanský, A., K. T. Smith, and J. Klembara. 2014. Variation in the position of the jugal medial ridge among lizards (Reptilia: Squamata): Its functional and taxonomic significance. Anatomical Record 297:2262–2272.
- Čerňanský, A., J. Klembara, and K. T. Smith. 2016. Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. Zoological Journal of the Linnean Society 176:861–877.
- Estes, R., K. de Queiroz, and J. A. Gauthier. 1988. Phylogenetic relationships within Squamata; pp. 119–281 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press, Stanford, California.
- Gauthier, J. A. 1982. Fossil Xenosauridae and Anguidae from the Lower Eocene Wasatch Formation, southcentral Wyoming, and a revision of the Anguioidea. University of Wyoming Contributions to Geology 21:7–54.
- Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. Bulletin of Peabody Museum of Natural History 53:3–308.
- Lee, M. S. Y., and J. D. Scanlon. 2002. Snake phylogeny based on osteology, soft anatomy, and ecology. Biological Reviews 77:333–401.
- Pregill, G. K., J. A. Gauthier, H. W. Greene. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. Transactions of the San Diego Society of Natural History 21:167–202.