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THE UNUSUAL TAIL OF *TETHYSHADROS INSULARIS* (DINOSAURIA, HADROSAUROIDEA) FROM THE ADRIATIC ISLAND OF THE EUROPEAN ARCHIPELAGO

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Abstract. The basal hadrosauroid *Tethyshadros insularis* from the uppermost Cretaceous of NE Italy lived on an island of the European archipelago in the Tethys Ocean. The tail of this dinosaur presents several apomorphic traits respect to the tails of other coeval hadrosauroids of the archipelago and of hadrosauroids in general. The estimated total length of the tail of the holotypic specimen shows that the tail was long, accounting for at least 56% of the total body length, relatively stiff and deep proximally, whereas it was whip-like distally. The reconstruction of the tail musculature by comparison with that of living archosaurs and other dinosaurs suggests that the posterior shift of the first haemapophysis affected the size and shape of the *M.m. caudofemorales* with important consequences on the locomotion of *T. insularis*. Somewhat peculiar stance and gait for this dinosaur are suggested also by limb features. The posterior shift of the vent and consequent longer distal tract of the intestine or a longer cloaca could increase the space for urine storage and urinary water reabsorption. The posterior shift of the vent could imply also longer oviducts and plausibly an increased number of eggs per clutch. Tail apomorphies of *T. insularis* may be related to the rugged and water-depleted karst landscape where the Italian dinosaur lived. The two main specimens of *T. insularis* differ in robustness possibly because of sexual dimorphism, ontogeny or high intraspecific variability.

INTRODUCTION

Complete and articulated caudal segments of the vertebral column of dinosaurs are extremely rare (Hone 2012). As a consequence, the actual tail length is usually unknown in most dinosaur taxa and it is object of interpretation in the skeletal reconstructions. Some complete and articulated skeletons of small-sized dinosaurs have shown that, when completely preserved, the tail is much longer than previously supposed (e.g., Herner 2009).

Traditionally, little attention has been given to vertebral column in the osteological and phylogenetic study of hadrosauroid dinosaurs (e.g., Wright & Lull 1942; Norman 2004; Horner et al. 2004). This because the vertebral morphology was considered to be very conservative within the hadrosauroids and the iguanodontians in general, with variability limited manly to the shape of the neural spine of the axis, degree of zygapophyseal development in the cervicals, number of cervical and sacral vertebrae, and elongation of the neural spines and chevrons (e.g., Horner et al. 2004; Prieto-Marquez 2010; McDonald et al. 2012b; Norman 2015). This

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lack of information is particularly true for the caudal vertebrae, which have usually been summarily described in the literature. However, caudal vertebrae are the most numerous elements in a hadrosauroid skeleton (with the possible exclusion of teeth) and therefore they are the ones that have the highest probability to be found in the fossil record as isolated elements.

Tail vertebrae can give information about the development of tail musculature, allowing hypotheses about locomotion and its ecological implications in extinct tetrapods (e.g., Persons & Currie 2011a-b, 2012 and 2014).

The preserved portion of the caudal vertebral column is articulated in the holotype of the non-hadrosaurid hadrosauroid *Tethyshadros insularis* Dalla Vecchia, 2009c from the basal part of the Liburnian Formation (upper Campanian or lower Maastrichtian) of NE Italy. Part of the tail is articulated also in a second referred specimen from the same locality and horizon. Furthermore, the tail of this dinosaur revealed to be an exception to the traditional view of the conservative morphology of the vertebrae, presenting several apomorphic traits (Dalla Vecchia 2009c).

Here, the tail features of *T. insularis* are described in detail, the total length of the tail of the holotype is estimated and the caudal vertebrae are compared with those of the other hadrosauroids from the latest Cretaceous European archipelago. The tail peculiarities of *T. insularis* are discussed and hypotheses about their functional and adaptive significance are advanced.

Institutional abbreviations – **AMNH**, American Museum of Natural History, New York, U.S.A.; **IPS**, Institut de Paleontologia Dr. Miquel Crusafont (currently Institut Català de Paleontologia "Miquel Crusafont," ICP), Sabadell, Spain; **IRSNB**, Institut Royal des Sciences Naturelles de Belgique, Brussels/Bruxelles, Belgium; **MB.R.**, Museum für Naturkunde, Berlin, Germany; **MCD**, Museu de la Conca Dellà, Isona, Spain; **MCSNT**, Museo Civico di Storia Naturale, Trieste, Italy; **MDE**, Musée des Dinosaures d'Esperaza, Esperaza, France; **MPZ**, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain; **NHMUK PV**, The Natural History Museum (former British Museum of Natural History), London, U.K.; **ROM**, Royal Ontario Museum, Toronto, Canada; **SC**, Italian State collections; **TMP**, Royal Tyrell Museum of Palaeontology, Drumheller, Canada.

Materials, terminology and methods

The material object of this study consists of the two specimens of *T. insularis* that preserve articulated segments of the vertebral column, namely the holotype SC 57021 (nicknamed "Antonio") and the referred specimen SC 57247 (nicknamed "Bruno"). In this paper, I use the numbers of the State collections that I attributed to the fossils in 1999 charged by the Ministero per i Beni Culturali ed Ambientali, and have already been reported in Dalla Vecchia (2008, 2009c). Personal observations on SC 57247 were made mainly on the unprepared specimen. SC 57247 was prepared in 2019, but it has not been made available for this study. However, photographs of the prepared specimen could be seen in the internet and the fossil was exhibited to the public in the winter 2019-2020 at the Duino Castle (Trieste), allowing some comparison.

The comparison with the material from the uppermost Cretaceous of Romania referred to *Telmatosaurus transsylvanicus* and deposited at the NHMUK, and with the hadrosauroid vertebrae from the Maastrichtian of Spain (Basturs Poble and Sant Romà d'Abella localities and partly Els Nerets) and France was based on the direct observation of the specimens. The specimen TMP 1998.058.0001 was also observed personally. Information about the specimens from the Maastrichtian localities of Costa de les Solanes, Arén and partly Els Nerets (Spain) is based on Prieto Márquez et al. (2019), Cruzado-Caballero (2012) and Conti et al. (2020), respectively. Information about the specimens from Limburg and Germany was also taken from the literature.

Following Sereno (1998), the Hadrosauroidea are all dinosaurs more closely related to *Parasaurolophus* than *Iguanodon*. In the phylogenetic analyses published during the last 12 years, *T. insularis* falls always within the Hadrosauroidea and outside the Hadrosauridae, but its phylogenetic affinities are somewhat variable. *T. insularis* forms a trichotomy with *Telmatosaurus transsylvanicus* and the Hadrosauridae in the strict consensus tree by Dalla Vecchia (2009c). It is nested in a more basal position in the Adams consensus tree of McDonald et al. (2012b: fig. 10), forming a trichotomy with *Levnesovia transoxiana* and the more advanced hadrosauroids (*Telmatosaurus transsylvanicus* results to be a hadrosaurid in this analysis). *T. insularis* is lower in the tree than the Hadrosauridae and their sister taxon *Telmatosaurus transsylvanicus* in the strict consensus tree of Norman (2015: fig. 50), being nested between *Probactrosaurus gobiensis* and *Levnesovia transoxiana* as the basal taxon of the Hadrosauromorpha (sensu Norman 2014).

T. insularis is the sister taxon of *Telmatosaurus transsylvanicus* and is lower in the tree than *Nanyangosaurus zhugeii* and *Zhanghenglong yangchengensis*, which are lower than the Hadrosauridae, in the simplified strict consensus tree of Wang et al. (2015: fig. 4); it has a similar relationships also in the strict consensus tree by Xing et al. (2014: fig. 13). *T. insularis* is the sister taxon of the Hadrosauridae and is higher in the tree than *Telmatosaurus transsylvanicus* in the strict consensus trees by Prieto-Márquez et al. (2016, 2019). *T. insularis* is the sister taxon of *Telmatosaurus transsylvanicus*, and *T. insularis* + *Telmatosaurus transsylvanicus* is the sister group of the Hadrosauridae, in the single most parsimonious tree of the analysis by Xu et al. (2018). Finally, *T. insularis* is placed between *Claosaurus agilis* and *Eotrachodon orientalis*, outside the Hadrosauridae and lower in the tree than *Telmatosaurus transsylvanicus*, in the strict consensus tree by Conti et al. (2000).

"Anterior" and "posterior" are used here in preference to "cranial" and "caudal" to avoid confusion, because this paper deals mainly with caudal vertebrae. Zygapophyses, parapophysis and diapophysis are considered in their original meaning of processes, not as synonym of zygapophyseal, parapophyseal and diapophyseal facets. Following Norman (1980: 43), the proximal caudal vertebrae are those with laterodorsal pleurapophyses (sensu Wild 1973: 62) on the centrum. Pleurapophyses are reported in literature also as "transverse processes" or "caudal ribs", but the transverse process and the caudal rib are two distinct components of the pleurapophysis which cannot be identified as such when they are fused to each other. The mid-caudal vertebrae are those without the pleurapophyses, but bearing haemapophyses (haemal arches or chevrons), whereas the distal caudal vertebrae lack pleurapophyses and haemapophyses. The neural arch is composed of the pedicels, zygapophyses and neural spine. The haemapophysis is composed of the pedicels and the haemal spine. The backward slope of the neural spines with respect to the vertical is the angle made by the line connecting the mid-point of the basal part of the spine and the mid-point of the apical part of the spine (in lateral view) with the elongation axis of the centrum minus 90°. The height of the centrum is measured about at mid-centrum from the ventral point of minimum central depth to the corresponding dorsal end of the centrum. Angles have been measured on digital images with the software ImageJ.

Following Romer (1977), the large intestine of extant archosaurs (crocodilians and birds), i.e., the straight portion of the intestinal tract between the ileum and the cloaca, is here reported as the colon.

The theoretical background of using the relationships between skeletal elements and soft tissues in extant archosaurs to infer these relationships in extinct dinosaurs is summarized in Ibiricu et al. (2014). Crocodilians and birds represent the two poles of the extant phylogenetic bracket (sensu Witmer 1995) for non-avian dinosaurs. Although birds share a more recent common ancestor with hadrosauroids than do crocodilians, they have an extremely reduced tail and a consequently specialized tail musculature (Gatesy 1995). Crocodilian tails more closely resemble those of the hadrosauroids in relative size, number of vertebrae, and development of processes for muscle attachment, but crocodilians are obligate quadrupeds with a prevailing sprawling posture. This must be considered when using the relationships between skeletal elements and soft tissues in extant archosaurs to infer these relationships in extinct dinosaurs, mainly when the latter are specialized taxa.

Specimens from Blasi site of Spain may be indicated with a Museum inventory number (acronym MPZ, Museo Paleontológico de la Universidad de Zaragoza) or a field number (acronym BLA).

The latest Cretaceous interval is considered to be composed of the Campanian and Maastrichtian Ages, 83.6-66 Ma.

SYSTEMATIC PALAEONTOLOGY

ORNITHOPODA Marsh, 1881
IGUANODONTIA Sereno, 1986
Hadrosauroidea Cope, 1869 sensu Sereno, 1986
Tethyshadros Dalla Vecchia, 2009c

Tethyshadros insularis Dalla Vecchia, 2009c

Figs. 1-6 and 16, SI figs. 1-4 and 6.

Holotype - SC 57021, nearly complete and articulated skeleton lacking part of the tail.

Referred specimens - SC 57022, SC 57023, SC 57025, SC 57026, SC 57247, SC 57256 (see Dalla Vecchia 2009c). All the specimens are at the MCSNT.

Distribution – Upper Campanian or lower Maastrichtian, Villaggio del Pescatore locality, Trieste Province, north-eastern Italy.

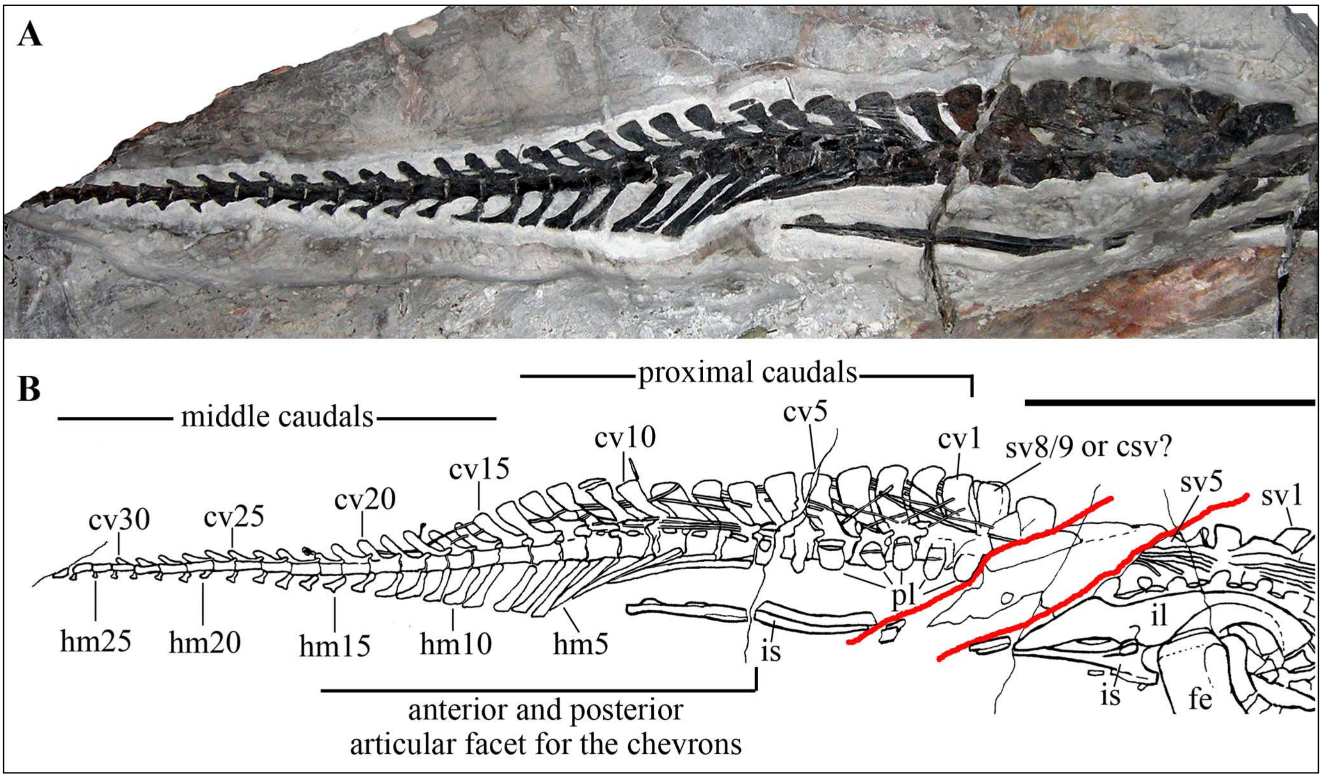

Fig. 1 - Caudal segment of the vertebral column of the holotype of *T. insularis* (SC 57021). A) Photograph; B) interpretative drawing. The red lines mark the synsedimentary fault displacing the caudal segment from most of the sacrum. Abbreviations: csv, caudosacral vertebra; cv1-30, caudal vertebrae 1-30; fe, right femur; hm 5-25, haemal arches 5-25; il, right ilium; is, right ischium; pl, pleurapophysis; sv1-9, sacral vertebrae 1-9. The scale bar equals 500 mm.

Description

The caudal vertebrae of the holotype of *Tethyshadros insularis* have been described by Dalla Vecchia (2009c). Only details useful for the comparison with the caudal vertebrae of the specimen SC 57247 and the other latest Cretaceous hadrosauroids of the European archipelago and for the discussion about the functional implications of the peculiar tail of *T. insularis* are considered here.

The tail of the holotype (Fig. 1) preserves the first 33 vertebrae, which are articulated, and is incomplete distally. The missing segment of the vertebral column remained in situ because the layer containing it was twisted by a fault and its extraction was difficult. The preserved segment of the caudal vertebral column is ca. 1650 mm long. It is disturbed and slightly dislocated at the caudal/sacral transition by a synsedimentary fault (see Fig. 1). The first caudal vertebra was considered the first one with a tongue-shaped pleurapophysis like those of the following proximal caudals. There are 13 or 14 proximal caudal vertebrae (it is unclear whether caudal 14 has a very small bump that can be considered a pleurapophysis or no process at all), followed by 20 or 19 mid-caudal vertebrae. A haemapophysis occurs between caudal vertebrae 32 and 33, thus the whole distal segment of the tail is missing and plausibly some mid-caudal vertebrae are also missing (probably as many vertebrae as the preserved ones, see below). Therefore, the tail of *T. insularis* is not “complete or near-complete” as suggested by Hone (2012: caption of tab. 2).

If not specified otherwise, the description of the anatomical details of the tail below is based on the holotype.

The specimen SC 57247 is a portion of an articulated and probably complete skeleton that was seriously damaged and partly destroyed during the field work in 1998. When recovered in 1999, it was composed of a main block (SC 57247A, Fig. 2), several smaller limestone blocks bearing various portions of the skeleton and hundreds of small bone fragments. Parts of the specimen remained exposed in situ and have been collected over 15 year later. According to press releases, blocks and fragments were later (2018) assembled and prepared by formic acid for exhibition purposes. As recovered in 1999,

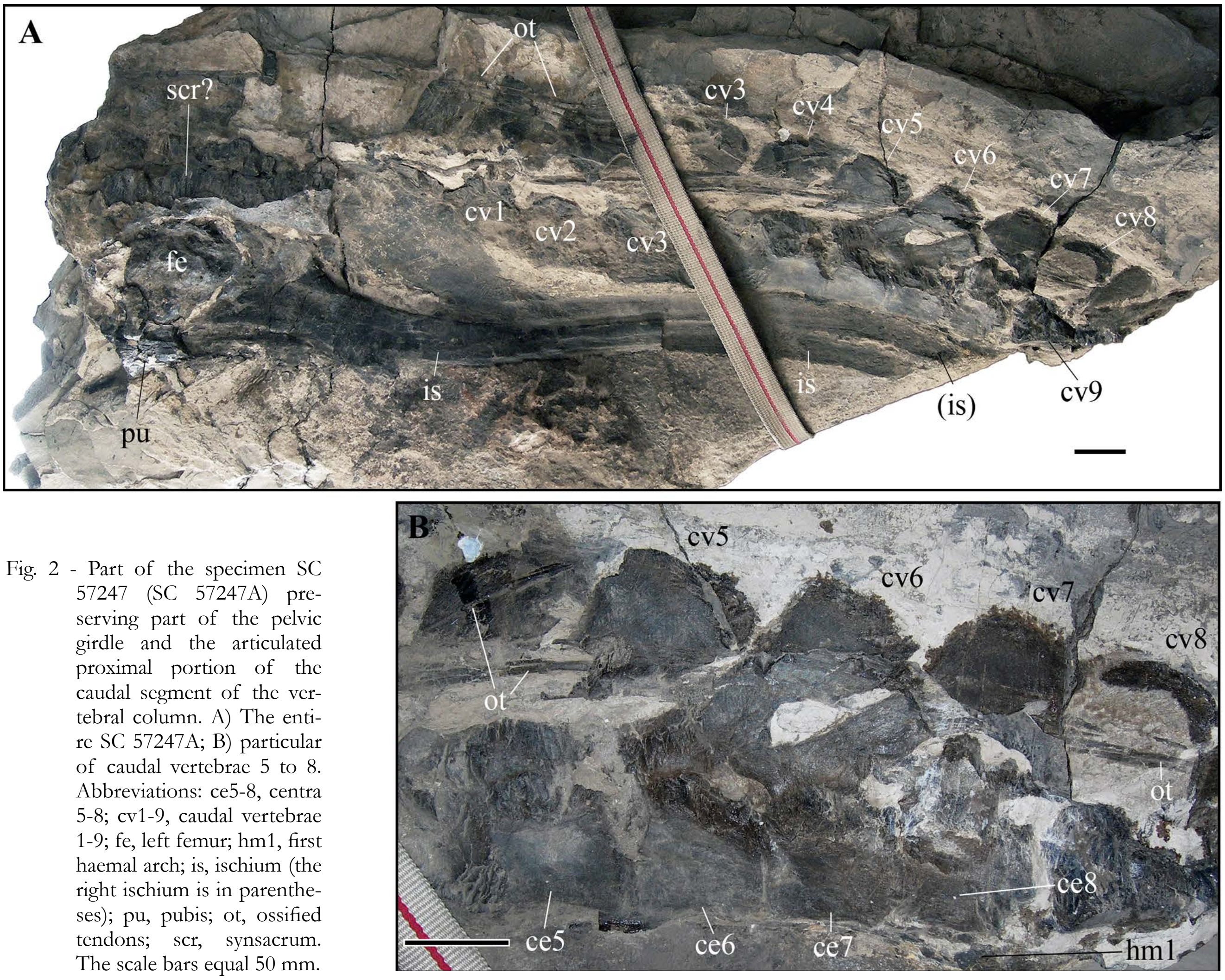

Fig. 2 - Part of the specimen SC 57247 (SC 57247A) preserving part of the pelvic girdle and the articulated proximal portion of the caudal segment of the vertebral column. A) The entire SC 57247A; B) particular of caudal vertebrae 5 to 8. Abbreviations: ce5-8, centra 5-8; cv1-9, caudal vertebrae 1-9; fe, left femur; hm1, first haemal arch; is, ischium (the right ischium is in parentheses); pu, pubis; ot, ossified tendons; scr, synsacrum. The scale bars equal 50 mm.

the surface of the main block contained the articulated proximal portion of the caudal vertebral column, which was composed of nine or ten vertebrae, part of the sacrum, part of the pelvic girdle ad the proximal portion of the articulated left femur (Fig. 2). Unlike the holotype, the ischia of this specimen are not stretched by a synsedimentary fault (Dalla Vecchia 2009c, fig. 5D), although the distal portions of the shafts are slightly displaced by a small fault. Photographs made available in the internet and other mass-media after preparation show that the proximal portion of the tail, from caudal 1 to 9 is composed of perfectly articulated vertebrae exposed in left lateral view. The first vertebra posterior to the fused sacral vertebrae is possibly a caudosacral. The tail is ~180° bent at level of vertebrae 9-10 and the tail segment posterior to vertebra 10 lies below and nearly parallel to the proximal segment. This unusual bending of the tail was caused some time after burial by the folding of the still plastic carbonate layer containing the specimen (see below). Caudal 10 is on the hinge of the fold and shows its left lateral side. The bent segment is made of 13 articulated vertebrae with their haemapophyses. Caudals 11-23 are ventrally and ventrolaterally exposed and dorsoventrally flattened. Neural arches are dorsoventrally compressed, thus the neural spines of caudals 11-18 and 21 project laterally from the left side of the vertebra and can be seen in left lateral view. This tail segment is slightly disarticulated at caudals 14-15; caudal 20 is just partially preserved because is damaged by a fracture. Between caudal 23 and the following vertebra (vertebra 24) there is a gap, probably because of the disarticulation of the tail. In fact, also the following caudal (vertebra 25) is isolated and separated from the most posterior vertebrae. The latter are located on a further fold of the layer (i.e., the specimen-bearing layer is folded S-wise). This distal portion of the preserved part of the tail is made, in anteroposterior order, of a single isolated vertebra like caudal 25 (exposed in ventral view), a series of 13 articulated vertebrae in ventral view, a detached segment of four articulated and smaller vertebrae possibly in lateral view and at least two scattered and more distal elements. Therefore, the total number of preserved vertebrae is at least 45 in SC 57247. The different sizes of the centra of the two posterior tail segments suggest that some vertebrae may be missing in between them.

Centra

Caudal centra are all longer than high along the whole series in both specimens (measurements of the holotype vertebrae are reported in SI, Tab. 1). This was considered an autapomorphy of *T. insularis* by Dalla Vecchia (2009c). From caudal 16 on, the length/height ratio (hereafter l/h) is ≥ 2 in the holotype. The shape of the centra changes along the tail. Centra bear pleurapophyses that project laterally at level of the centrum-neural arch boundary (Fig. 3) at least up to vertebra 13, possibly up to vertebra 14. A sharp longitudinal ridge runs along the whole dorsal part of each of the lateral surfaces of the centrum in the following vertebrae 15-19 (Fig. 4B-C; SI, Fig. 1). These lateral ridges make hexagonal the centrum in anterior and posterior views. In vertebrae 20-25, the lateral ridge gradually migrates dorsally toward the dorsolateral margin of the centrum; in these centra, a groove separated the ridge from the dorsolateral margin of the centrum (SI, Fig. 2A). The lateral ridge and groove disappear in caudal 26 (SI, Fig. 2A). Practically, the upper lateral side of the hexagon gradually fades into the dorsal side. The centra of caudal vertebrae 23 to 33 have the shape of a hemicylinder with the convex side ventral, the wide flat side dorsal and semicircular articular facets (SI, Fig. 2). The hemicylindrical centra are twice broader than high (SI, Tab. 1), as it can be appreciated in vertebra 32, where the posterior articular facet is 27 mm wide and 13 mm high (not considering the projecting processes for the haemapophyses; SI, Fig. 2B). The centra are probably broader than high at least starting from caudal 15.

Centra are amphicoelous at least starting from vertebra 8; the articular facets of the last 15 vertebrae are deeply concave (SI, Fig. 2B-D). They are such also in SC 57247. The posterior articular facet of centrum 32 apparently shows a small and circular facet on its upper left corner (SI, Fig. 2B-C), but it is unclear whether it is a real vertebral feature or an artefact of preparation. The lateral surfaces of the centra appear to be nearly flat in the first vertebrae; they are concave from at least caudal 9 to 14. They are concave ventral to the longitudinal ridge in vertebrae 15 to 17 or 18. The ventral margin of the centra in lateral view is markedly concave in centra 18-33.

The posterior processes for the chevrons are well developed in all of the preserved centra starting from caudal vertebra 7. Articular facets for the pedicels of the haemal arches occur also at the anteroventral corner of the centrum at least up to vertebra 22.

Intercentral spaces are evident posterior to caudal 8 (Fig. 4) and range from 0 (between centra 14-15) to ca. 7.5 mm (e.g., between centra 23-24) in length. Intercentral spaces are variable because of the slight displacements of the centra, although all of the vertebrae are articulated at level of the zygapophyses.

The centra of the first caudals of SC 57247 are also longer than high, but their elongation is

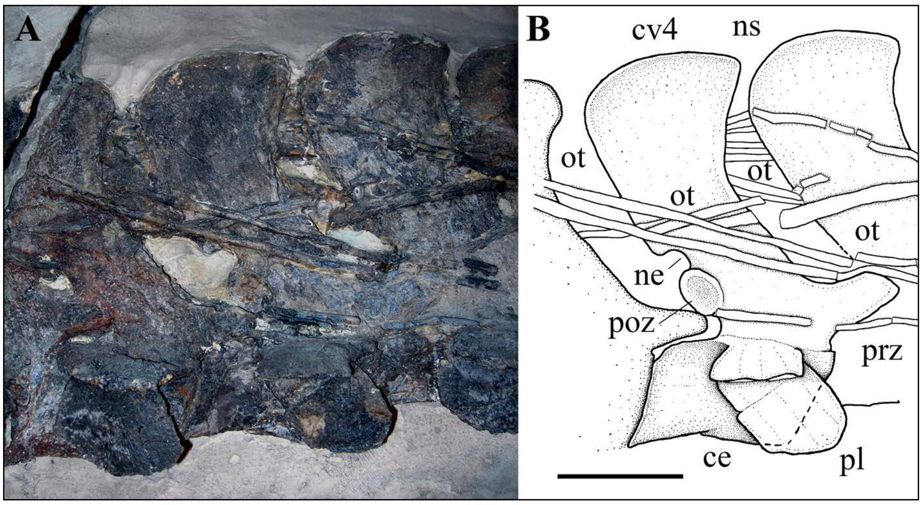

Fig. 3 - Proximal caudal vertebrae of the holotype of *Tethyshadros insularis* (SC 57021) with meat cleaver-like neural spines and tongue-like pleurapophyses. A) Photograph; B) interpretative drawing of caudal vertebra 4. Abbreviations: ce, centrum; cv4, caudal vertebra 4; ne, 'neck'; ns, neural spine; pl, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis; ot, ossified tendons. The scale bars equal 50 mm.

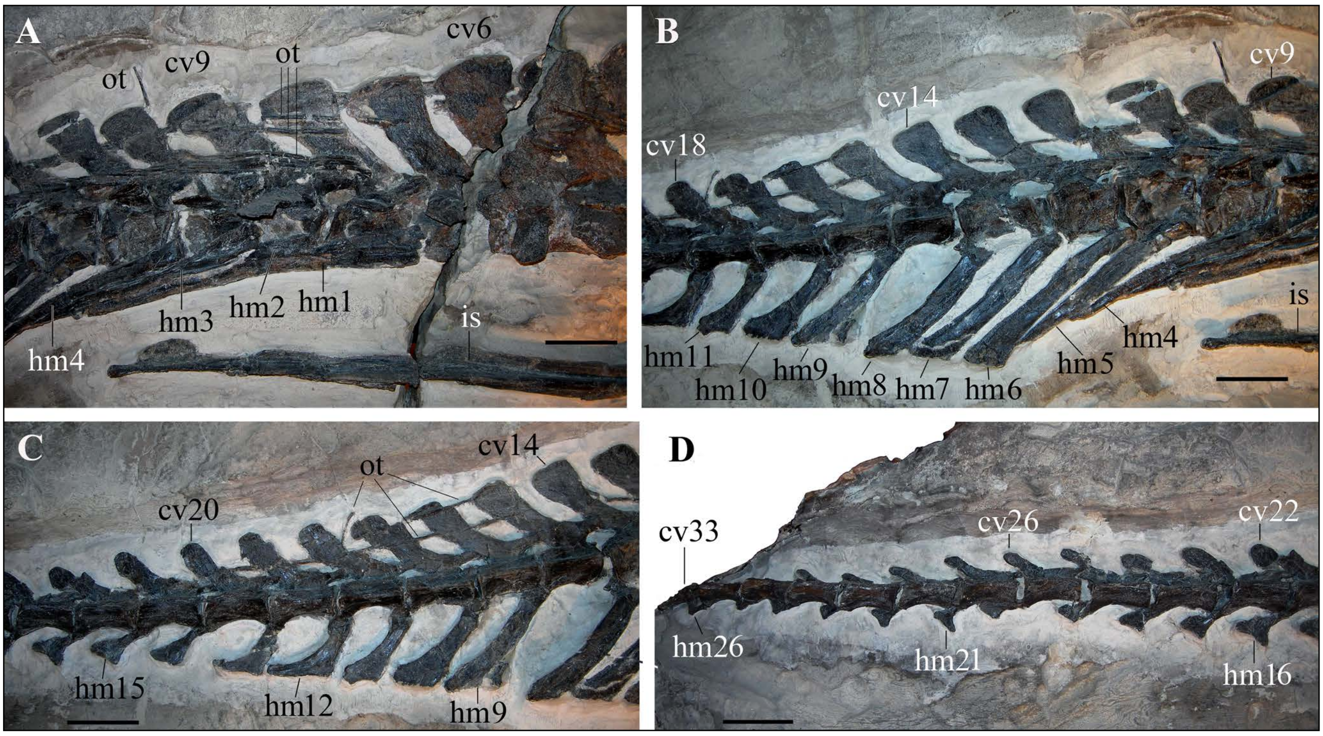

Fig. 4 - The articulated caudal vertebrae of the holotype of *Tethyshadros insularis* (SC 57021) from caudal 6 to 33. A) Segment 6-11; B) segment 11-18; C) segment 15-22; D) segment 23-33. Abbreviations: cv6-33, caudal vertebrae 6-33; hm1-26, haemal arches 1-26; is, ischium; ot, ossified tendons. The scale bars equal 50 mm.

minor and centra appear to be more massive than those of the holotype. The centra of caudal vertebrae 5-7 were 60-61 mm long and 53-53.5 mm high (l/h was 1.13-1.15, before preparation), whereas caudal 5 is 65 mm long with l/h = 1.51 in the holotype (SI, Tab. 1). Also the centra of the bent segment of the tail of SC 57247, corresponding to vertebrae 10-23, and those of the following isolated caudal vertebrae 24 and 25, appear as more massive than the corresponding centra of the holotype. However, these vertebrae are exposed in ventral view in SC 57247, whereas those of the holotype are visible in lateral view, thus differences may be just apparent. Caudal centrum 12 of SC 57247 has two small and paired neurovascular foramina set in the middle on the ventral side. There is practically no intervertebral space between the centra in the perfectly articulated first 13 caudal vertebrae of SC 57247, indicating that intervertebral disks were thin, if present.

Pleurapophyses

In the holotype of *T. insularis*, the pleurapophyses occur at least up to vertebra 13. Vertebra 14 is damaged, thus the presence or the absence of the pleurapophysis cannot be checked. The pleurapophyses of caudal vertebrae 1-5 are tongue-shaped, very broad anteroposteriorly, flattened dorsoventrally and directed laterally (Figs. 1, 3 and 5). The pleurapophyses of caudals 2-5 had broke in the proximal part and the distal fragment is turned ventrally (Figs. 3 and 5). The pleurapophyses of the following vertebrae 6 and 8-11 (the pleurapophysis of caudal 7 is broken and missing) are not much reduced in lateral extent respect to the preceding, but they are much narrower anteroposteriorly and with a marked constriction at mid-shaft (SI, Fig. 3). It is impossible to establish how much restoration affected the shape of these pleurapophyses, which are partly reconstructed (SI, Fig. 3B). Vertebrae 12 and 13 (possibly vertebra 14 too) present only a small, wing-like, lateral knob (Fig. 4B; SI, Fig. 1A).

The pleurapophyses of the exposed left side of SC 57247 were all missing in the original block SC 57247A (Fig. 2), but they are preserved in the prepared specimen. They can be identified at least up to caudal 12. Assuming that they originated from the preparation of the counter-block of SC 57247A and are not totally reconstructed, they appear to be slightly different from those of the holotype. In fact, the pleurapophyses of SC 57247 are spatula-shaped (narrow proximally and much expanded distally) instead of tongue-shaped, at least up to caudal 5. In the first five caudal vertebrae, the caudal ribs are apparently unfused to their transverse processes; some of them have been wrongly glued to the centra ventral to the short transverse processes. All of the pleurapophyses posterior to caudal 5 and the single caudal ribs (if they are not broken pleurapophyses) are damaged or partly preserved and reconstructed; thus, their apparent shape may be misleading and should be considered carefully.

Neural spines

The neural arches and neural spines of the most proximal caudal vertebrae are the tallest of the entire vertebral column, but are not much higher than those of the distal dorsal vertebrae. In caudal vertebra 4 of the holotype (Fig. 3), the heights of the neural arch and neural spine are 2.7 and 2.1 times the centrum height, respectively. The tallest is the neural arch of caudal 3, posterior to which the height decreases gradually. However, the neural arch of caudal 7 is slightly lower than those of caudals 5 and 8 and the neural arches of caudals 11 and 12 are slightly higher than that of caudal 10. This originates two shallow depressions along the dorsal profile of the tail on caudals 7 and 10 (Fig. 1). The decrease in height of the neural arches is greater from caudals 12 to17 where the tail reduces much of its depth. The neural arch of vertebrae 20 to 30 is very low and small (Fig. 4D; SI, Fig. 2A); it is broken and missing in caudal 32, where the narrow neural canal is exposed, and fragmentary in caudal 31 (SI, Fig. 2C-D). In these vertebrae, the neural arch is set on the middle of a flat and broad dorsal side of the centrum (SI, Fig. 2C-D).

The neural spines of caudal vertebrae 1 to 5 or 6 (the neural spine of caudal 6 is damaged) are anteroposteriorly wide, laterally flat and meat cleaver-shaped (wrongly reported as "hatched-shaped" [sic] in Dalla Vecchia 2009c: 1107), with a 'neck' just dorsal to the postzygapophyses (Figs. 1, 3 and 5). These neural spines are slightly recurved forward. The neural spines of the last dorsal and sacral vertebrae are probably similar to those of the first caudals (Dalla Vecchia 2009c). The neural spines of caudal vertebrae 7 to 17 are fan- or spatula-shaped in lateral view, flaring apically with a slightly convex dorsal margin, inclined posteriorly and slightly recurved (Figs. 1 and 4A-C; SI, Fig. 1 and 3A). The apical expansion of the neural spine practically ends with caudal 17 and the expansion gradually decreases after caudal 14 (Fig. 4B-C; SI, Fig. 1), which is possibly the last vertebra with a hint of a pleurapophyses. The neural spines of the following caudals have a 'petaloid' outline with a rounded apex and a maximum anteroposterior width which is reached before the apex (Fig. 4C-D; SI, Fig. 2A). These petaloid neural spines are straight and inclined backward (Figs. 1 and 4B-D). Neural spine 18 has a transitional shape (SI, Fig. 1B). The posterior slopes of the neural spines with respect to the vertical in caudals 4, 8, 15, 19 and 26 are about 24°, 47°, 45°, 36° and 60°, respectively.

In SC 57247 (Fig. 2), the neural spines of the caudal vertebrae are similar to those of the holotype, although they show some minor differences. Caudals 5-7 are better preserved than in the holotype, showing that the transition from the meat cleaver-shaped and spatula-shaped neural spines is gradual from caudal 4 to 6. The dorsal margin of spines 5 to 8 is concave in the middle (in lateral view) making heart-shaped the expanded dorsal portion of the spine. This is not the case of the holotype (Figs. 4a and 5). The neural spines of caudals 5-9 are slightly more inclined posteriorly than the corresponding in the holotype. The spine of caudal 9 of SC 57247 is less expanded apically than those of the preceding caudals and its dorsal margin is rounded; the apical portion of the spine of caudal 9 of the holotype is more expanded and 'cut'. In SC 57247, the spines of the following caudals 10-17 are similar to that of caudal 9, with a slight constriction at mid-spine in lateral view.

Zygapophyses

Zygapophyses are still articulated each other in all of the vertebrae except in caudals 4 and 5. The prezygapophyses are relatively long and slender, whereas the postzygapophyses are extremely short. The rounded articular facet of the postzygapophysis of caudal 4 faces lateroposteriorly and slightly ventrally (Fig. 3). The articular facets of the zygapophyses are nearly vertical, at least through caudal 26, thus a limited lateral movement was allowed to the tail. The articular facets of the zygapophyses are sub-vertical at least up to caudal vertebra 10 in SC 57247A.

Haemal arches (chevrons)

The first haemal arch articulates between cau-

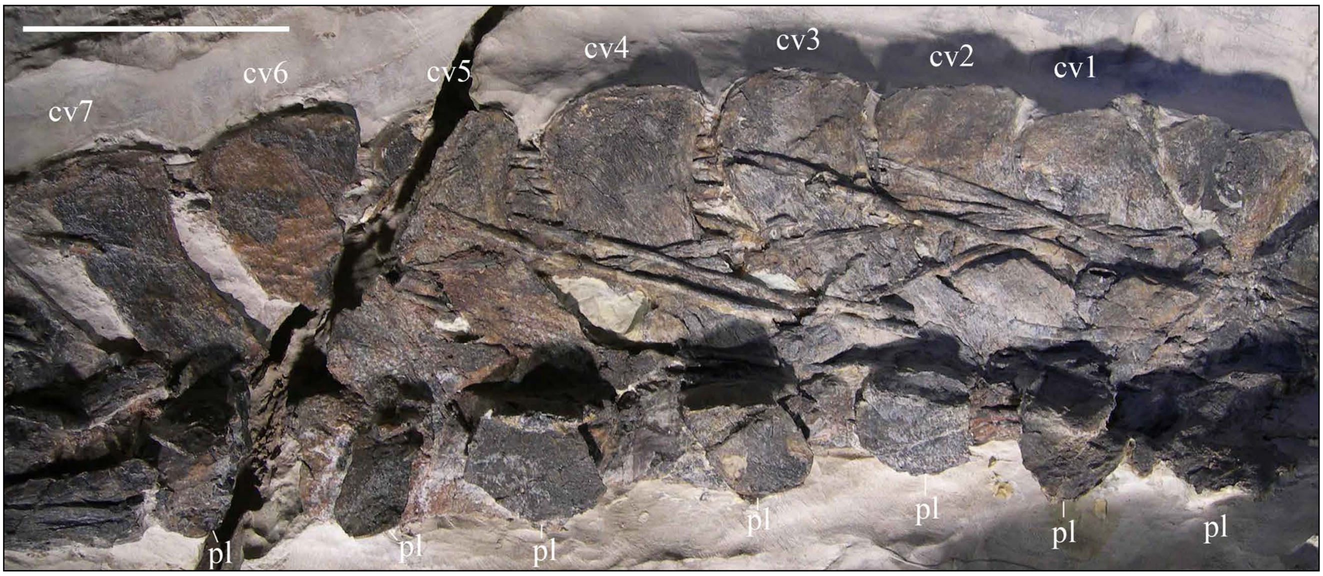

Fig. 5 - Proximal caudal vertebrae 1-7 of the holotype of *Tethyshadros insularis* (SC 57021) and their broad pleurapophyses. Abbreviations: cv1-7, caudal vertebrae 1-7; pl, pleurapophysis. The scale bars equal 100 mm.

dal vertebrae 7 and 8 (Fig. 1) in the holotype. The position of this haemal arch corresponds to the first fully fan-shaped neural spine. All of the following 25 haemal arches are articulated to the corresponding centra (Fig. 4). Haemal arch 3 and partly also haemal arch 1 are rotated and shows their Y-like shape in anteroposterior view; the others are exposed in right lateral view, excluded haemal arch 2 that is overlapped by haemal arches 1 and 3. The haemal arches change in shape along the vertebral series. Haemal arches 1-5 have long and rod-like haemal spines which are only slightly compressed transversely and taper distally. Haemal arches 1-4 are slightly recurved. Haemal arches 1-5 slope posteriorly in a way that each one contacts the following (Figs. 1 and 4A-B). The higher backward slope of the first haemal arches with respect to the following others corresponds to the slope of the distal end of the ischia (i.e., the first haemal arches and distal end of the ischia are more or less parallel to each other; Fig. 1).

Haemal arch 1 is the longest (250 mm); length decreases gradually from haemal arches 6 (143 mm long) to 26. The distal ends of the haemal spines of haemal arches 6 to 26 are anteroposteriorly expanded (Fig. 6). The distal expansion is asymmetrical and skewed backward in haemal arches 6 to 13, giving the haemal arch a boot-like shape in lateral view (Fig. 6A-F; they are asymmetric chevrons, according to the definition by Otero et al. 2012). This asymmetry is incipient in haemal arch 6 and increases up to haemal arch 12 (Figs. 4C and 6A-E), whose backward expansion of the spine is longer than the rest of the haemapophysis and contacts the anterior side of the following haemal arch (Fig. 6E). Haemal arch 13 (which is articulated to caudals 19 and 20) is similar to haemal arch 12 (Fig. 6F) and shows a pattern of fine diagonal scarring on the lateral surface of the spine (Fig. 6F); this scarring can be observed also in chevrons 8-11 and probably is present in all distally expanded haemapophyseal spines. Haemal arches 14 to 26 are shorter than the preceding ones and have a somewhat bilobate (forked, according to the definition by Otero et al. 2012) distal expansion of the spine (Fig. 6G-K). This expansion is slightly asymmetrical in haemal arch 14, which bears a longer posterior lobe (Fig. 6G), whereas the lobes are more or less symmetrical in the successive haemal arches; however the posterior lobe is longer again in the last preserved haemal arch (Fig. 6K). The first haemal arches are much longer than the neural arches of the corresponding vertebrae, then the disproportion decreases gradually and lengths are similar in corresponding neural arches and haemal arches starting from about haemal arch 14 on.

The haemal arches were not evident in the unprepared SC 57247A (Fig. 2). After assemblage and preparation, haemal arches are preserved at least up to caudal 24. Haemal arches are exposed in lateral view, except haemal arches 9, 11-13, and ?19 which are exposed in anterolateral or posterolateral views, showing both pedicels. The first three haemal arches

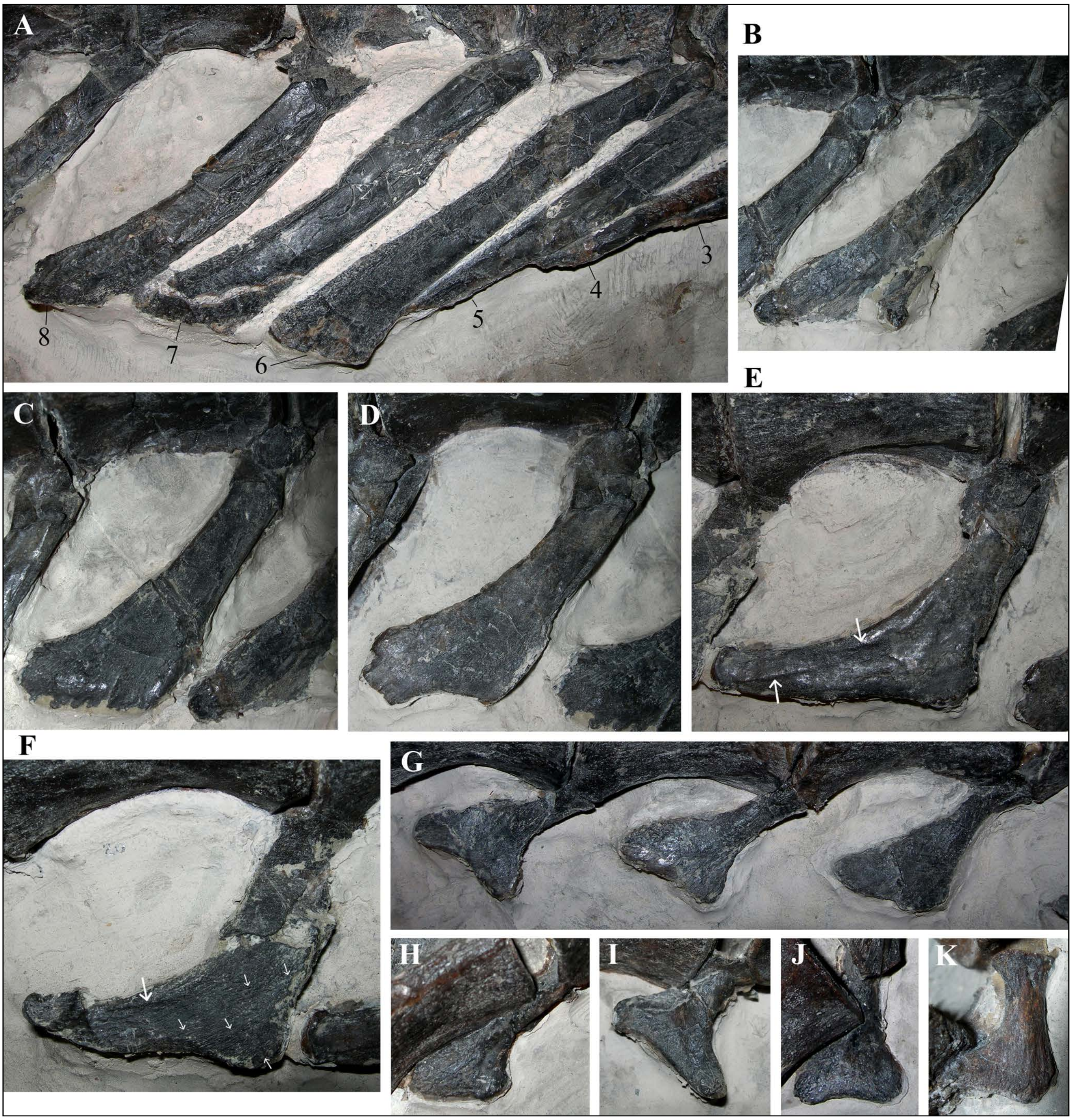

Fig. 6 - Haemapophyses of the holotype of *Tethyshadros insularis* (SC 57021), right lateral view. Haemapophyses A) 3-8; B) 9; C) 10; D) 11; E) 12; F) 13; G) 14-16; H) 20; I) 21; J) 22; and K) 26. Larger arrows point to the ridges on haemapophyses 12 and 13; smaller arrows point to the fine scarring on haemapophysis 13. Not drawn to scale. As for scale, see Figure 4.

occur in the hinge zone of the layer fold. Haemal arches 2 and 3 are articulated to caudals 9/10 and 10/11, respectively. Haemal arch 1 crosses haemal arch 2 at mid-shaft and is detached from its articulation with caudals 8/9. Therefore, the first haemal arch appears to occur in a slightly more distal position respect to the holotype. However, the caudosacral was counted as the first caudal vertebra in SC 57247A. In the holotype, the partially preserved vertebra before the first caudal (Fig. 1) could be the last sacral (as supposed by Dalla Vecchia 2009c) or a caudosacral; in the latter case, the position of the first haemal arch would be the same in the two specimens. The first three haemal arches are shorter and more robust than those of the holotype, but their spine is incompletely preserved distally;

they are rod-like and their spines have an elliptical cross-section. Haemal arches 4 and 5 are articulated with caudals 11/12 and 12/13, respectively. The following haemal arches are slightly detached and shifted from their anatomical articulation with the centra. As there are seven intervertebral joints and eight haemal arches, there is one in excess haemal arch (possibly one of the two below the centrum of caudal 14, i.e. haemal arches 7 and 8), which can be explained as an artefact of preparation. This should be kept in mind when reading the following description. Haemal arch 4 appears to be complete and is the longest among the completely preserved haemal arches, which gradually reduce in length along the tail. It is rod-like with a straight spine that is slightly and symmetrically expanded at its distal extremity. Haemal arches 5 and 6 are like haemal arch 4, but shorter. Haemal arch 6 is slightly shifted anteriorly relative to its anatomical position and the distal extremities of haemal arches 4-6 contact each other. The spine of haemal arch 7 is slightly recurved backward and is symmetrically expanded distally resembling a spoon, whereas the distal end of haemal arches 8 and 9 is asymmetrical expanded posteriorly (boot-like). The following haemal arches 10-13 have rounded and symmetrically expanded extremities, therefore they are very unlike the boot-like haemal arches of the holotype (Fig. 6C-F).

Ossified Tendons

The ossified tendons are wire-like and occur epaxially in the proximal and mid-tail, as well as in the dorsum and sacrum, on both sides of the vertebral column. The posteriormost ossified tendon ends on the anterior margin of the neural spine of caudal 20 at mid-spine; it is located at the beginning of the dorsoventral lowering of the tail to a whip-like aspect and in correspondence of the passage from boot-shaped to bilobate chevrons (Fig. 4C). Ossified tendons cross diagonally the neural spines in caudal vertebrae 1 to 6, arranged in an irregular rhomboidal cross-lattice pattern (Fig. 5; SI, Fig. 4). The thin ossified tendons have probably been affected by the preparation by acid, partly splitting away during preparation; the preserved sample is only a part of the original lattice. This is suggested by the scars left by the missing tendons on the right lateral side of the neural spines.

Three sets of ossified tendons can be identified on the right lateral side of the proximal neural spines of caudal vertebrae 1 and 2, whereas only two occur in the following caudals 3-6 (SI, Fig. 4). One set runs posterodorsally inclined of 17.5-22° with respect to the axis of the tail (number of measurements, N = 5; mean, M = 19°) overlapping a set running posteroventrally and slightly less inclined (9°-16.5°; N = 3; M = 11.5°). These are identified as the tendons of the *M. semispinalis* of the *M. transversospinalis* system in other iguanodontoideans (Organ 2006); specifically, the medial set belongs to the *M. articulospinalis*, whereas the lateral set to the *M. tendinoarticularis*. The third set is the most medial of the three and is represented by a few and thinner tendons running posterodorsally at a low angle (~10°); these tendons can be identified only on the first and second caudal vertebrae (SI, Fig. 4) and are plausibly those of the *M. spinalis*, which also belongs to the *M. transversospinalis* system, and are medial to the other ossified tendons (Organ 2006). Apparently, the *M. spinalis* tendons are scarcely ossified or not ossified at all in the holotype of *T. insularis*. From dorsals 7 to 14 on the right side of the tail, ossified tendons are only posterodorsally directed. At the base of the neural spines of caudals 8 to 13, just above the zygapophyses, a bundle of at least four ossified tendons runs posterodorsally nearly parallel to the axis of the tail (SI, Fig. 3A). Two tendons running posterodorsally across spines 7-9 (SI, Fig. 3A) are also inclined at very low angles (ca. 2.6° and 3.2°). Because of their development, these are plausibly the lateral tendons of the *M. semispinalis* (i.e., those of the *M. tendinorticularis*; cf. Organ 2006).

The two tendons spanning vertebrae 15-18 run posteroventrally (Fig. 4C; SI, Fig. 1), thus they plausibly are the medial tendons of the *M. semispinalis*. One of these two tendons crosses the middle of the spines, whereas the other runs in a more apical position and possibly originates from the posterodorsal corner of neural spine 15. They are inclined 8° and 12.5°, respectively. A detached short tendon segment occurs near neural spine 10; another one crops out from the left side of neural spine 18 (Fig. 4A and C; SI, Fig. 1B). The last preserved tendon runs at the level of the lower part of the neural spine at least along vertebrae 18-20 (Fig. 4C). It slopes posteroventrally, although it is nearly parallel to the axis of the tail, thus it is a medial tendon of the *M. semispinalis*. Ossified tendons run posteroventrally at low angle also along the left side and can be seen in the gaps between the neural spines. The irregular arrangement of the ossified tendons was probably caused by muscular decay, as suggested by the presence of detached elements.

Two bundles of long ossified tendons were visible in the proximal part of the tail of the unprepared SC 57247A up to caudal 9 (Fig. 2). One bundle ran along the dorsal half of the neural spines of the posterior sacrals and first caudals (up to about caudal 3). The apparent direction of the tendons was posteroventral at very low angle. The other bundle ran along the middle of the neural spines starting about at caudal 2 and reaching caudal 8. Only a single tendon crossed the neural spine of caudal 9. The apparent direction of the tendons of this second bundle was initially posterodorsal at low angle, then tendons curved to be nearly parallel to the axis of the tail and finally they were directed posteroventrally at low angle. One single tendon crossed neural spine 4 posterodorsally at high angle, possibly inserting to the posterior apical corner of neural spine 5 (Fig. 2). After preparation, the pattern is the same, although some missing segments of the tendons have probably been reconstructed. The two bundles meet in correspondence of caudals 2-3. At least six ossified tendons can be counted on the lateral surface of neural spine 3. The most posterior ossified tendon occurs on spine 10 and is single and thinner than the proximal ones. The longest tendon spans vertebrae 2 to 8, but portions may have been reconstructed. One tendon apparently inserts on the anterior side of the base of neural spine 9. The other insertions are unclear due to the overlapping of the tendons, but they are apparently located at mid-spine. Therefore, ossified tendons do not form a regular rhomboidal lattice in SC 57247; they are more numerous proximally (mainly on the sacrum and first caudals) and decreases in size and diameter moving posteriorly. Orders of overlapping tendons cannot be reliably identified.

Distal to caudal 10, i.e., posterior to the flexure of the tail, no ossified tendons can be observed in the prepared specimen; this could be a preservational bias or a consequence of the preparation by acid, which makes unstable and very fragile thin bones as the ossified tendons are, leading to their destruction.

Estimate of the total tail length of the holotype of *Tethyshadros insularis*

According to Hone (2012), caudal vertebrae count in ornithischian dinosaurs is probably less variable than in the saurischians and it appears to be generally consistent within hadrosaurs. Hadrosauroids are considered to have 50 to 70 tail vertebrae (Norman 2004; Horner et al. 2004). However, very few specimens preserve the complete distal portion of the caudal segment of the vertebral column (Hone 2012). Therefore, the lower count of 50 vertebrae is probably taphonomically biased or underestimated. For example, the specimen IRSNB 1551 of *Mantellisaurus atherfieldensis* (see Norman 2015) preserves only 33 caudal vertebrae and its tail was reported as “almost complete” by Norman (1986: 308). However, the last preserved vertebra bears a chevron (Norman 1986: fig. 2), thus it is a mid-caudal and at least the entire distal segment of the tail is missing in that specimen. Specimen IRSNB 1551 preserves 15 proximal caudals and only 18 mid-caudals (Norman 1986). Therefore, also some mid-caudal vertebrae are missing.

The most complete tail of the basal iguanodontian *Tenontosaurus tilletti*, which preserves 60 vertebrae but lacks the last distal elements, has eight proximal caudals, 22-32 mid-caudals and 28-38 distal caudals (uncertainty in the count of mid and distal caudals is due to the uncertainty on the position of the last chevron; Forster 1990). One specimen of the hadrosaurid *Edmontosaurus regalis* (ROM 5851) from the lower part of the Horseshoe Canyon Formation (uppermost Campanian) near Drumheller (Alberta, Canada) was reported to have 76 tail vertebrae (Lull & Wright 1942), but unfortunately it was never described. The specimen TMP 1998.058.0001 (Fig. 7), belonging to a small indeterminate hadrosaurid from the Dinosaur Provincial Park (Alberta, Canada) (Brinkman 2014; Persons & Currie 2014) preserves one of the most complete hadrosauroid tails ever discovered. It comes from the Dinosaur Park Formation (upper Campanian, underlying the Horseshoe Canyon Formation), where *Edmontosaurus* is not reported (Campione & Evans 2011), therefore it plausibly belongs to a distinct genus. The articulated tail of TMP 1998.058.0001 was broken into

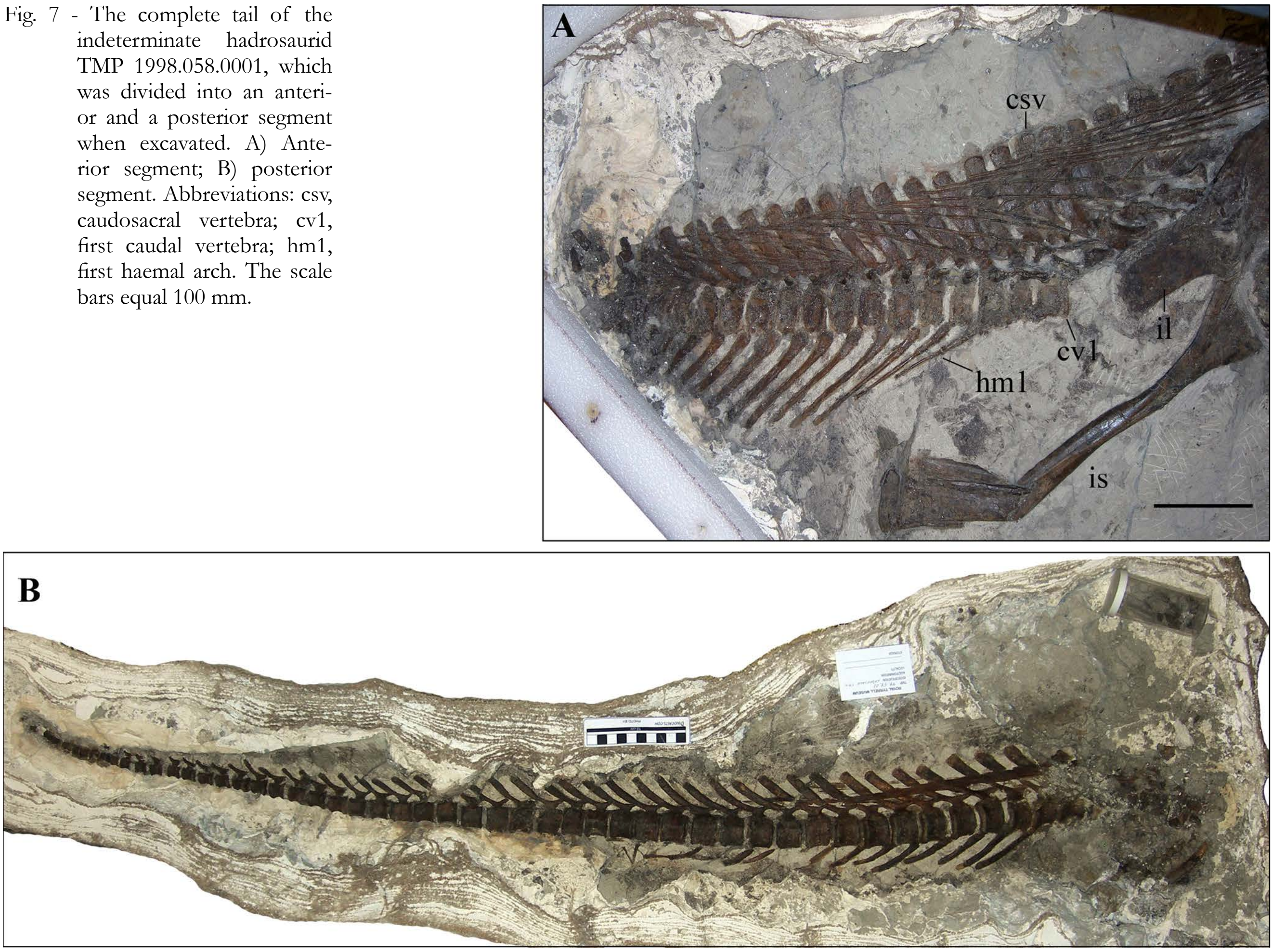

Fig. 7 - The complete tail of the indeterminate hadrosaurid TMP 1998.058.0001, which was divided into an anterior and a posterior segment when excavated. A) Anterior segment; B) posterior segment. Abbreviations: csv, caudosacral vertebra; cv1, first caudal vertebra; hm1, first haemal arch. The scale bars equal 100 mm.

two segments during field work and about ten of the first mid-caudal vertebrae are damaged (Fig. 7). This tail is composed of 77 vertebrae (pers. obs., 2011). There are a caudosacral vertebra (with pleurapophyses contacting the postacetabular process of the ilium), at least 14 proximal caudal vertebrae (vertebrae at the mid-proximal transition are damaged and unprepared) and over 25 mid-caudals. The first chevron is located between caudals 3 and 4. This specimen is used here as a reference to estimate the length of the missing portion of the tail of SC 57021, under the assumption that both had originally the same total count of caudal vertebrae.

The ratios between the length of each caudal centrum and the length of the preceding centrum in caudals 9 to 33 were calculated in SC 57021 and range 0.86-1.07 (SI, Tab. 1). The mean ratio from caudals 9 to 33 (0.98; it means that the centrum of vertebra x+1 is 98% the length of the centrum of the preceding vertebra x) is similar to the mean of the last 12 vertebrae (vertebrae 22-33; 0.9775), thus there is no evident increase in shortening in the distal part of the segment. I used this ratio (0.98) to estimate the length of each of the missing centra 34-77 (SI, Tab. 2, estimate A). The sum of these lengths is 1009.94 mm. As the spaces left by the intervertebral discs are short in the articulated segment, this sum well approximates the total length of the missing segment, but is anyway a minimum estimated length that is somewhat lower than the actual length.

The ratio between the length of each caudal centrum and the length of the preceding one in the tail of TMP 1998.058.0001 was also calculated (SI, Tab. 3). The mean of this ratio calculated in caudal vertebrae 25 to 77 is 0.99, but the ratio ranges 0.79-1.12 and an increase in centra shortening is evident in the distal part of the tail as the mean ratio of the last 11 preserved centra is 0.92 (SI, Tab. 3).

I used the ratios of vertebrae 34-77 of TMP 1998.058.0001 to estimate the length of each of missing centra 34-77 of SC 57021 (SI, Tab. 2,

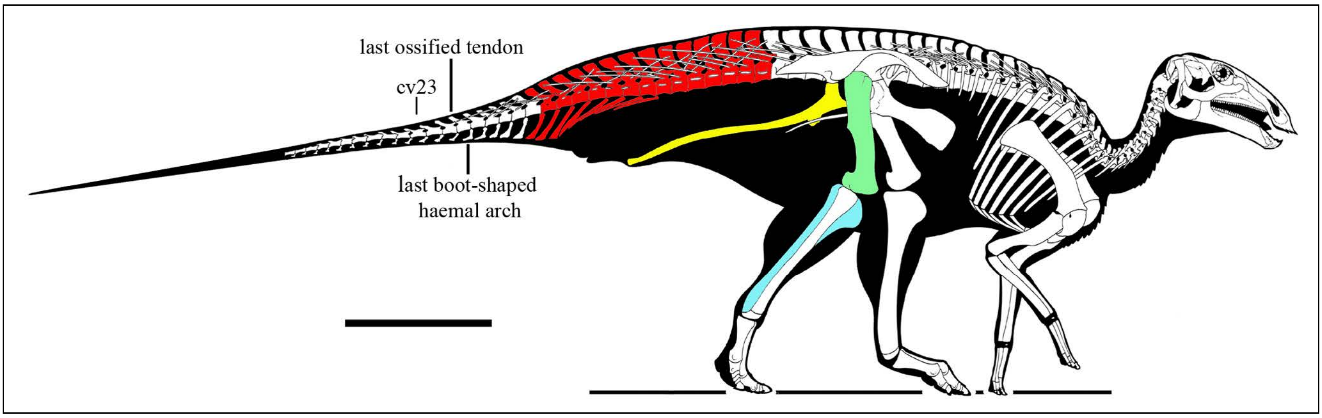

Fig. 8 - Reconstruction of the skeleton of the holotype of *Tethyshadros insularis* with the silhouette of the portion of the tail that is probably missing in the fossil. The proximal caudals and their haemapophyses are evidenced in red; the ischium is yellow; the femur is green; and the tibia is pale blue. Artwork by M. Auditore (modified). The scale bar equals 500 mm.

estimate B). Since the lengths of centra 68, 72 and 76 of TMP 1998.058.0001 are unknown, the mean ratio of the last ten measurable centra of TMP 1998.058.0001 (0.93) was used to calculate the missing ratios. The sum of those lengths is 885.78 mm (nearly 125 mm less than the estimate based on the mean ratio of caudals 9 to 33 of SC 57021). This estimate of the missing portion of the tail of SC 57021 is probably more accurate than that based only on the ratios from the preserved part of the tail, because accounts for the increase in shortening of the centra that probably occurred in the terminal portion of the tail. When added to the preserved portion (1650 mm; Dalla Vecchia 2009c), the tail of the holotype of *T. insularis* results to be 2535.78 mm long (1650+885.78 mm) and appears to be somewhat whip-like (Fig. 8). The total body length measured from the tip of the snout to the distal end of the tail results to be 4505.78 mm (the preserved part of the skeleton is 3620 mm long; Dalla Vecchia 2009c). The tail accounts for 56% of the total body length and is over 3.5 times the length of the trunk.

The tail/femur ratio would be 6.04, much higher than the ratio reported by Hone (2012) for *T. insularis* and much higher than that of all other hadrosauroids in table 2 of Hone (2012), ranging 3.7-3.1 (included TMP 1998.058.0001; 3.7). This rather high ratio is due also to the comparatively shorter femur of SC 57021, as suggested by the low femur/humerus ratio (1.46, whereas this ratio ranges 1.66-2.10, with mean 1.90, in a sample of 15 North American hadrosaurid specimens; Lull & Wright 1942).

CAUDAL VERTEBRAE OF OTHER LATEST CRETACEOUS HADROSAUROIDS FROM THE EUROPEAN ARCHIPELAGO

During latest Cretaceous times, most of present-day central and southern Europe was an archipelago of islands in the Tethys Ocean between the Afro-Arabian continent to south, the North European landmass to north and the Asian continent to east (Philip et al. 2000; Csiki-Sava et al. 2015). According to the palaeogeographic reconstruction by Philip et al. (2000; Fig. 9), the Adriatic Island where *T. insularis* lived was much smaller than the Ibero-Armorican Island, which was the largest island of the archipelago and corresponds to the present day Iberian Peninsula plus most of France. The Adriatic Island was possibly slightly larger than the closer Tisia-Dacia Island (corresponding to the present day north-western part of Romania).

No complete and articulated hadrosauroid skeletons comparable to those from the Villaggio del Pescatore site have yet been discovered in the uppermost Cretaceous of Europe. Anyway, caudal vertebrae of hadrosauroid dinosaurs allowing comparison with the *T. insularis* material are reported from the uppermost Cretaceous of Romania, Spain, France, Belgium and the Netherlands, and Germany. Most of this material was still undiscovered, unpublished or had been summarily described in the literature when *T. insularis* was published in 2009.

Romania

Several caudal vertebrae from the Densuş-

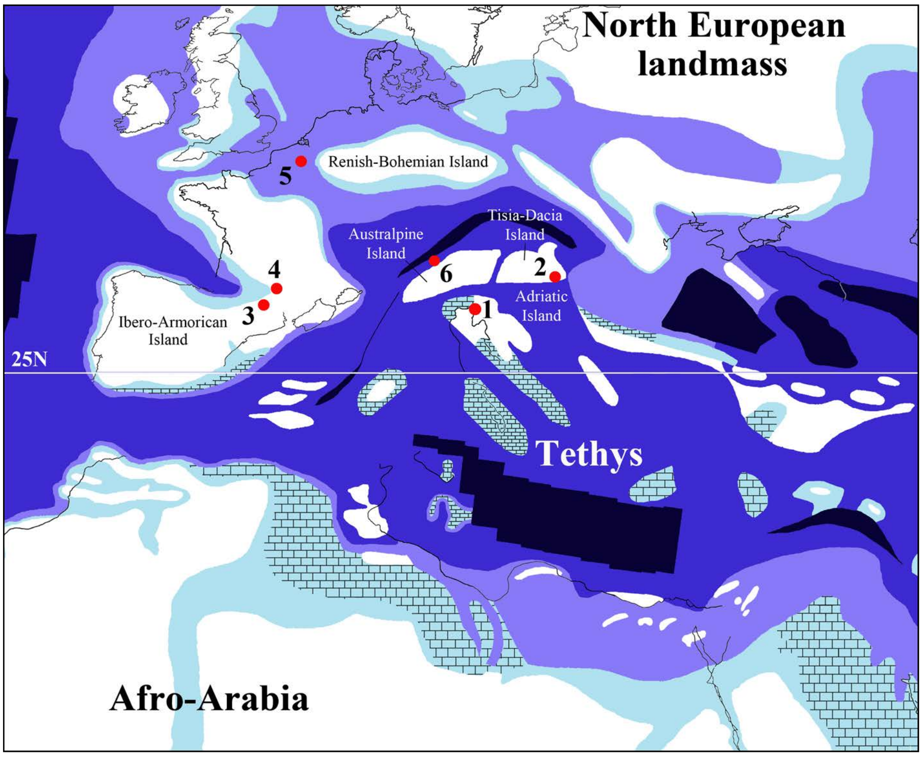

Fig. 9 - Location of the latest Cretaceous localities that yielded the caudal vertebrae of hadrosauroid dinosaurs mentioned in the text. The late Maastrichtian palaeogeographic map of the European archipelago is based on Philip et al. (2000), modified. 1) Villaggio del Pescatore (Italy); 2) Haţeg Basin (Romania); 3) the Tremp Syncline localities (Spain); 4) the Southern France localities; 5) the Limburg localities (the Netherlands and Belgium); and 6) Bad Adelholzen locality (Germany). White indicates emergent land; pale blue, shallow sea; pale blue with brick fabric, carbonate platforms; lilac, the Chalk Sea; blue, deep sea; dark blue, oceanic basins (oceanic crust). Present day coastlines of Europe, northern Africa and the Arabian Peninsula are reported as reference.

Ciula and Sâmpetru Formations of the Haţeg Basin, Transylvania, have been referred to the basal hadrosauroid *Telmatosaurus transsylvanicus* (see Nopcsa 1915, 1928; Dalla Vecchia 2014; pers. obs.). All of the hadrosauroid material from the uppermost Cretaceous of Transylvania has been traditionally referred to *Telmatosaurus transsylvanicus* (e.g., Therrien 2005; Benton et al. 2010). However, the fossil-bearing units span the whole Maastrichtian and possibly part of the upper Campanian (Csiki-Sava et al. 2016); furthermore, most of the material referred to *Telmatosaurus transsylvanicus* do not show any diagnostic features of this taxon (see Dalla Vecchia 2006, 2009a). Dalla Vecchia (2009a) suggested referring the not-typical hadrosauroid material from the uppermost Cretaceous of Transylvania to *Telmatosaurus transsylvanicus* with reserve; this suggestion was later followed by Prieto-Márquez (2010) and Csiki-Sava et al. (2016). The only nearly complete caudal vertebra to have been be referred to *Telmatosaurus transsylvanicus* in the literature is a proximal caudal (NHMUK PV R. 4915; Fig. 10A) from the Vălioara locality of the Densuş-Ciula Formation (Nopcsa 1928; Dalla Vecchia 2009b). The type material of *Telmatosaurus transsylvanicus* is from Sacel locality of the Sâmpetru Formation and does not include caudal vertebrae (Nopcsa 1900; Dalla Vecchia 2006, 2009b), thus NHMUK PV R. 4915 cannot be a priori referred to *Telmatosaurus transsylvanicus*. Like the caudals of *T. insularis*, the amphicoelous centrum of NHMUK PV R. 4915 is longer than high (l/h at mid-centrum is ca. 1.35). It has anterior and posterior processes for the haemapophyses, and the posterior processes are more prominent than the anterior. There are pleurapophyses, although they are broken. These features indicate that NHMUK PV R. 4915 is a proximal element, but posterior to the vertebra bearing the first chevron. The zygapophyseal articular facets are nearly vertical. The neural spine is laterally compressed, slightly recurved and nearly upright. The neural spine is incipiently meat cleaver-shaped, with a ‘neck’ at the base and the upper portion that is moderately expanded anteroposteriorly, but not much expanded apically as those of the first proximal caudals of *T. insularis*. The upper 4/5 of the spine has rough posterolateral and apical surfaces. The ‘neck’ is basoapically longer than in the meat cleaver-shaped neural spines of *T. insularis*; the neural arch is comparatively as tall as that of caudal 4 of *T. insularis* holotype but the neural spine is proportionally lower (the heights of the neural arch and neural spine are 2.67 and 1.68 times the centrum height, respectively).

A second caudal vertebra, NHMUK PV R.4973 (Fig. 10B), from the Sâmpetru Formation near Sâmpetru, lacks most of the neural spine. It was figured in Nopcsa (1928: pl. 5, fig. 5) with

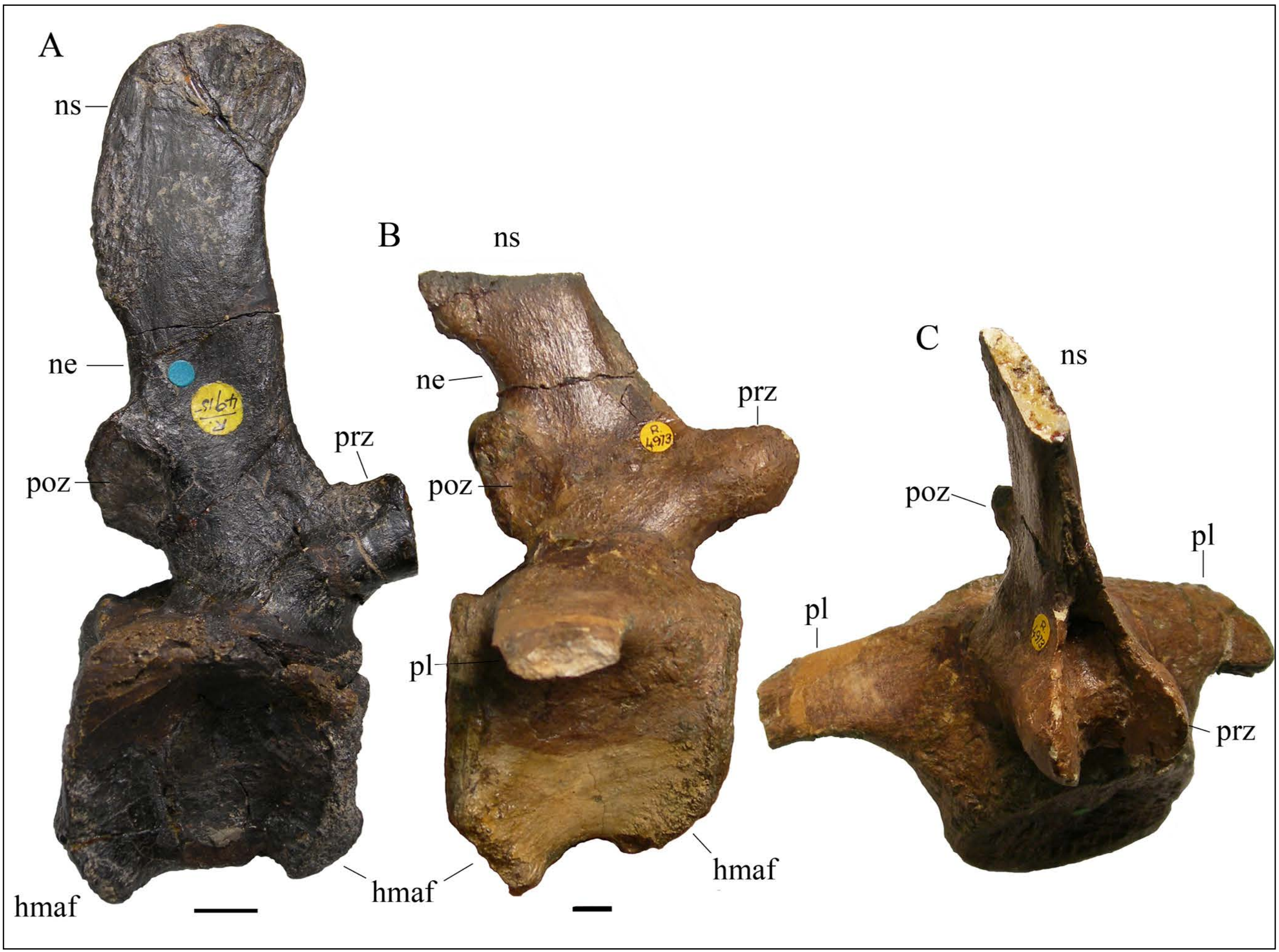

Fig. 10 - Proximal caudal vertebrae from the uppermost Cretaceous of Transylvania (Romania). A) NHMUK PV R. 4915, right lateral view; B) NHMUK PV R.4973, right lateral view; and C) NHMUK PV R.4973, right anterodorsal view. Abbreviations: hmaf, articular facet for the haemal arch; ne, 'neck'; ns, neural spine; pl, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis. The scale bars equal 10 mm.

the neural spine reconstructed on the basis of the neural spine of NHMUK PV R. 4915. This second vertebra is similar to NHMUK PV R. 4915, with a 'necked' basal part of the neural spine and asymmetrically developed anterior and posterior processes for the chevrons on the centrum, but it is larger, less elongated (l/h at mid-centrum is ca. 1.20) and the neural spine is more inclined backward. Both pleurapophyses lack their distal ends; the preserved part is anteroposteriorly narrow, dorsoventrally flat and slightly dorsoventrally arched (Fig. 10C).

In the sample of caudal centra referred to *Telmatosaurus transsylvanicus* at the NHMUK and at the Muzeul Civilizației Dacice și Romane of Deva (Romania), there are neither mid-caudal centra as elongated as centra 23 to 33 of *T. insularis* nor centra with the shape of amphicoelous hemicylinders (pers. obs.).

Spain

The oldest hadrosaur remains from the Conca Dellà area, in the Tremp Syncline of NE Spain, come from the Els Nerets site of the La Posa Formation, which is referred to the magnetochron C31r and dated to the early Maastrichtian (Conti et al. 2020). Ten hadrosaurid caudal vertebrae are reported from this site (Conti et al. 2020: 3) and three of them are figured (Conti et al. 2020: fig. 5I-P). These remains were referred to an unnamed lambeosaurine hadrosaurid showing affinity with the Tsintaosaurini, although the phylogenetic analysis produced to test the affinities of this unnamed taxon does not find support for a clade Tsintaosaurini (Conti et al. 2020: fig. 9).

The three figured specimens are nearly complete proximal caudal vertebrae (MCD-8638, IPS-NE-13 and MCD-6690), whereas the other seven

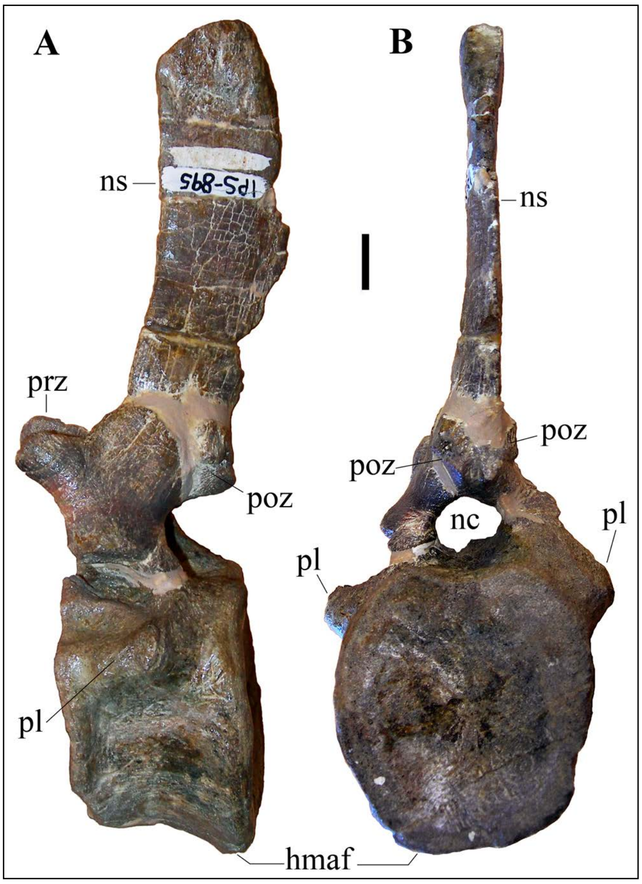

Fig. 11 - Proximal caudal vertebra IPS-NE-13 from the lower Maastrichtian Els Nerets locality of Conca Dellà, Spain. A) left lateral view; B) posterior view. Abbreviations: hmaf, articular facet for the haemal arch; nc, neural canal; ns, neural spine; pl, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis. The scale bar equals 10 mm.

are fragmentary specimens (MCD-61 to 63, MCD-65 and 66, MCD-5209 and MCD-7095), which are neither figured nor described. Although IPS-NE-13 and MCD-6690 are reported as mid-caudals by Conti et al. (2020), they preserve traces of the pleurapophyses and hence are proximal caudals. The three figured specimens have similar small sizes (centra are 40, 36 and 40 mm long in MCD-8638, IPS-NE-13 and MCD-6690, respectively). According to the measurements reported in Conti et al. (2020: tab. 1) and fig. 5J, L and M, the centra of the nearly complete vertebrae are much taller than long, especially in MCD-8638 and IPS-NE-13.

MCD-8638 is probably the first caudal vertebra because it has an anteroposteriorly short and opisthocoelous centrum with sub-circular articular facets (Conti et al. 2020: fig. 5I), there is no reference to the presence of articular facets for the chevrons in its description and it presents a wing-like proximodorsal part of the anteroposteriorly compressed pleurapophyses (see vertebra MDE-Les1-5 from Lestaillats 1 locality of France below). The neural spine is twice as tall as the centrum, elliptical in cross-section and "thicker proximally than distally" (Conti et al. 2020: 7). The neural spine is upright, but it is backward recurved; in lateral view, it enlarges slightly in the basal segment, maintains a moderate anteroposterior width for most of its basoapical length and tapers slightly apically. The apex of the neural spine is blunt but not club-shaped (the spine is laterally flat and is not thickened apically).

IPS-NE-13 (bearing also the acronym IPS-845; Fig. 11) is proportionally more elongated than MCD-8638 and has an amphicoelous centrum with hexagonal articular facets and facets for the chevrons (Conti et al. 2020: 7). Therefore, it is from a more distal position in the tail. Conti et al. (2020: 7) retains that the caudal ribs were not fused to the transverse processes in this vertebra, but what they interpret as "square facets for attachment of the transverse processes" are probably the worn-out proximal part of the broken pleurapophyses. The latter have sub-rectangular cross sections that are craniocaudally longer than dorsoventrally high. The pleurapophyses of this vertebra were more massive than those of *T. insularis*. The tall neural spine of IPS-NE-13, which lacks the apical portion, is slightly recurved and anteroposteriorly wider than that of MCD-8638 but is unlike the apically expanded spines of *T. insularis*. This neural spine also lacks the basal 'neck' of the first caudals of *T. insularis* and the Transylvanian taxon (Fig. 10A-B).

The deformed MCD-6690 has an amphicoelous centrum like IPS-NE-13 (Conti et al. 2020: 7), but it is proportionally more elongated. Furthermore, its neural spine is proportionally much taller (over three times as tall as the centrum) and anteroposteriorly narrower and it "expands and thickens distally" (Conti et al. 2020: 7). Apparently, MCD-6690 belongs to a different taxon with respect to the other two proximal caudals from Els Nerets locality.

The type material of the lambeosaurine *Pararhabdodon isonensis* come from the Tossal de la Doba locality (reported as Sant Romà d'Abella in the literature) of the Conca Dellà zone (Dalla Vecchia et al. 2014). It is from the uppermost Maastrichtian Talarn Formation, which originated during the magnetochron C29r (Fondevilla et al. 2019). The sample includes a nearly complete proximal caudal

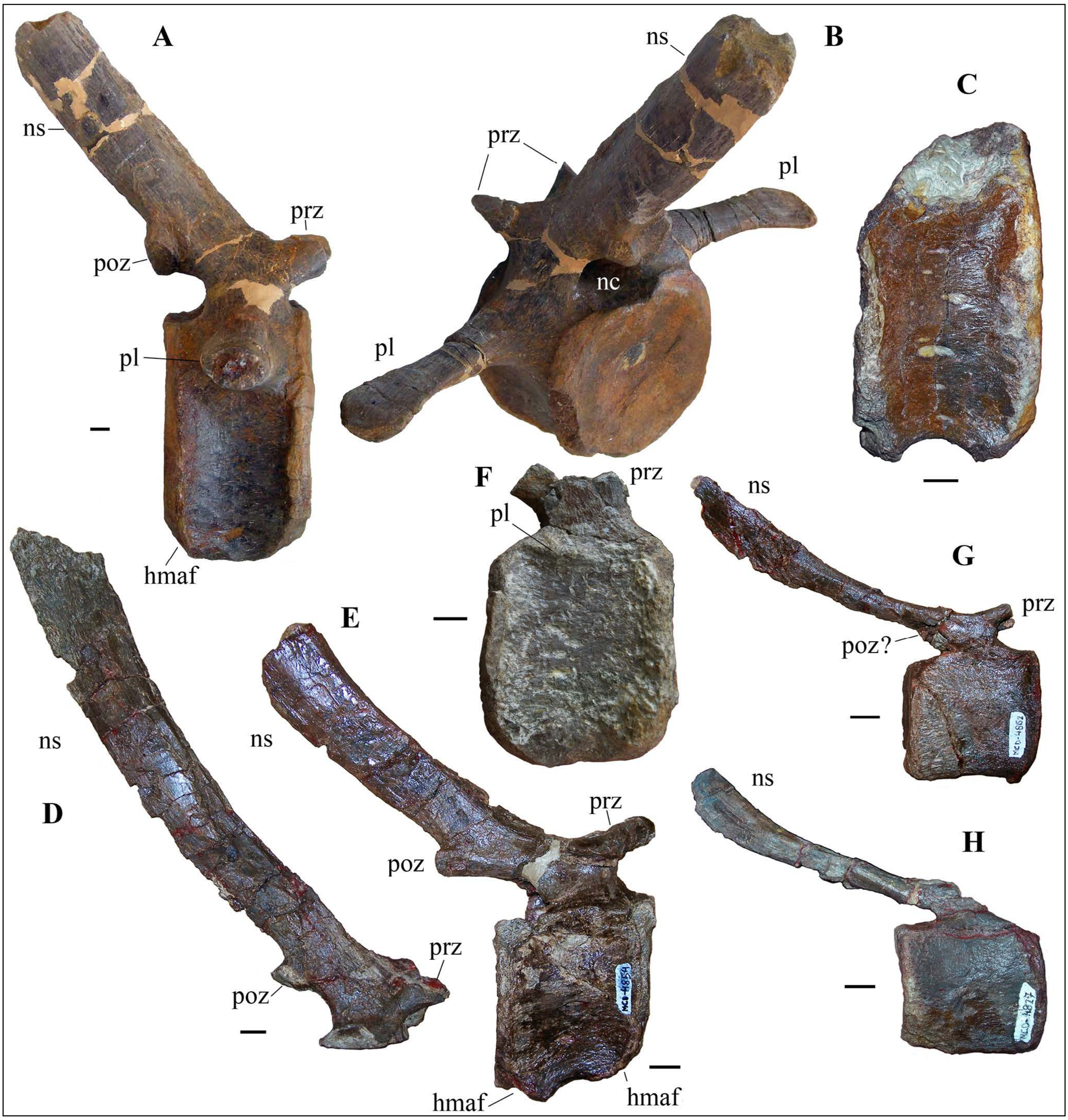

Fig. 12 - Caudal vertebrae from the Maastrichtian Tossal de la Doba (A-B; *Pararhabdodon isonensis*) and Basturs Poble (C-H; Lambeosaurinae indet., lateral views) localities of Conca Dellà, Spain. A-B) IPS-695-5, proximal caudal in right lateral and left posterodorsal view, respectively; C) MCD-5117, proximal caudal centrum; D) MCD-4928, nearly complete neural arch of a proximal caudal vertebra; E) MCD-4854, posterior proximal caudal; F) MCD-5112, one of the last proximal caudal vertebrae, right lateral view, but mirrored; G) MCD-4862, mid-caudal vertebra; and H) MCD-4827, mid-caudal vertebra. Abbreviations: hmaf, articular facet for the haemal arch; na, neural arch; ns, neural spine; pl, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis. The scale bars equal 10 mm.

vertebra (IPS-695-5, centrum height is 115 mm; Fig. 12A-B), four proximal caudal centra and five mid-caudal centra (see Dalla Vecchia et al. 2014 for the list of the museum numbers). These vertebrae had been found associated and were referred to a single individual (Casanovas-Cladellas et al. 1999), but the provenance of some of the caudal centra is dubious (Dalla Vecchia et al. 2014). Because of its long pleurapophyses and the sub-circular articular facets of the centrum, IPS-695-5 is one of the first proximal caudals. However, it is not one of the chevron-less most proximal caudals, having well-developed posterior facets for the haemal arch. It is probably the first chevron-bearing vertebra of the tail. Its centrum is much higher than long (l/h at mid-centrum is ca. 0.63). The pleurapophyses have an anteroposterior constriction in the middle and a distal expansion (Fig. 12B) like those of caudals 9-11 of the *T. insularis* holotype, but they are comparatively longer, slender and dorsoventrally thicker than those of *T. insularis*, and have a circular proximal cross section. Unlike the proximal caudals of *T. insularis*, the preserved basal portion of the neural spine is anteroposteriorly narrow in lateral view, has parallel anterior and posterior margins and lacks a basal 'neck' (Fig. 12B). The backward slope of the neural spine is 40°.

Remains of at least 50 disarticulated and scattered caudal vertebrae (including also isolated centra and neural arches) belonging to several distinct individuals have been found in the Basturs Poble bonebed of the Conca Dellà zone. Only a few of them preserve the centrum associated with the neural arch (pers. obs.). The Basturs Poble bonebed occurs in the Conques Formation and is stratigraphically lower than the close Tossal de la Doba locality, but higher than the Els Nerets locality (Conti et al. 2020: fig. 2); it is plausibly late early Maastrichtian in age (magnetochron C31r; Fondevilla et al. 2018). The hadrosauroid remains from this bonebed have been tentatively referred to *Pararhabdodon isonensis* by Fondevilla et al. (2018), because of the stratigraphic range of this taxon, which was reported also from the very close Serrat del Rostiar-1 locality by Prieto-Márquez et al. (2013; based on the maxilla MCD-4919). The Serrat del Rostiar-1 bone-bearing horizon is approximately the lateral equivalent to the Basturs Poble bonebed (see Fondevilla et al. 2018). However, Prieto-Márquez et al. (2019: 33) have subsequently referred MCD-4919 to "Tsintaosaurini indeterminate" and have erected the new basal lambeosaurine *Adynomosaurus arcanus* from the same horizon at the nearby Costa de les Solanes locality. Consequently, the Basturs Poble bonebed sample should now be referred to an indeterminate lambeosaurine. Most of the caudal vertebrae from the Basturs Poble bonebed are small-sized, the centra ranging 25.3-65.5 mm in length, with 80% of the centra that are less than 45 mm long. Evidence of immaturity is common within the sample: the neural arches are unfused to the centra in some vertebrae (e.g., MCD-4764, MCD-4832, MCD-4853, MCD-4883a,c, MCD-4961, MCD-4975, MCD-4979 and MCD-4997; probably this is also the case of most of the isolated neural arches), whereas the neurocentral suture is still partly visible in others (MCD-4774, MCD-4824, MCD-4862, MCD-4890 and MCD-4921).

The proximal centra are rather short and tall (see for example, MCD-5117 with l/h at mid-centrum < 0.74; Fig. 12C). In lateral view, the neural spines of the proximal caudals are tall, ribbon-like, slightly recurved and have prespinal and postspinal laminae (Figs. 12D-E). They gradually broaden apically, but the apical anteroposterior expansion is moderate. The neural spines are laterally flattened and not club-shaped (i.e., they are not much transversely thickened apically) and there is no 'neck' at their bases. The centrum of the posterior proximal vertebra MCD-4854 (Fig. 12E) is higher than long (l/h is 0.93) and bears anterior and posterior articular facets for the pedicels of the haemal arches; the posterior facets are set on prominent processes. The backward slope of the neural spine is about 45°. The pleurapophysis of the vertebra MCD-5112 (Fig. 12F) is a thin longitudinal ridge, suggesting that this is one of the last proximal caudals. Its centrum is higher than long (l/h is ca. 0.90). The anterior mid-caudals (Fig. 12D-E) have centra that are moderately longer than high (l/h is 1.15 and 1.18 in MCD-4862 and MCD-4827, respectively). Their neural spines are long and very slender and their apical portions are slightly recurved. The basal part of the neural spine has a sub-circular cross-section, whereas the apical portion is slightly expanded anteroposteriorly and flattened laterally. The anterior margin of the expanded portion is thicker than the blade-like posterior margin. The backward slope of the neural spine is about 60°. These caudal vertebrae differ from those of *T. insularis* in the minor elongation of their centra and shape and size of their neural spines.

The few chevrons from the Basturs Poble bonebed are mostly from the proximal part of the tail and are fragmentary. The most complete haemal arches (SI, Fig. 5A-D) are ribbon-like (finger-like; Persons et al. 2014), with anteroposteriorly narrow spines that are flattened laterally and extremely long dorsoventrally. They are straight to moderately recurved in lateral view and there is no evidence of a distal expansion. One ribbon-like chevron is recurved backward (SI, Fig. 5E-F), but its curvature could be augmented by taphonomic factors; its spine is unexpanded distally. This may be one of the first haemal arches, which are shorter, more inclined backward and sometimes more recurved than those immediately following along the tail in hadrosaurids (cf. Paul 2010: figs at pp. 299, 304, and 307-309). No boot-shaped or bilobate chevrons have been collected from the Basturs Poble bonebed.

The Costa de les Solanes locality has yielded the holotype and referred material of *Adynomosaurus arcanus*, including three fragmentary caudal vertebrae (Prieto-Márquez et al. 2019). Specimens have been identified by Prieto-Márquez et al. (2019) as a proximal caudal centrum (MCD-7141; not figured), a mid-caudal (MCD-7127, Prieto-Márquez et al. 2019: fig. 4I) and a distal caudal (MCD-7142, Prieto-Márquez et al. 2019: fig. 4G and H) vertebra. The proximal caudal centrum is described as "craniocaudally compressed" (Prieto-Márquez et al. 2019: 23). The mid-caudal vertebra is composed of a centrum that is higher than long (l/h is about 0.79, based on fig. 4I) and an incomplete and separated neural spine with the postzygapophyses. It is unclear whether the neural spine is apically complete or not. If it is complete, it is moderately tall (twice as tall as the centrum), nearly straight, laterally flattened and moderately flaring apically in lateral view like the posterior proximal caudal MCD-4854 from Basturs Poble site (Fig. 12E), although the postzygapophyses appear to be much larger. Because the rest of the neural arch is not preserved, the slope of the spine is unknown. The centrum of the purported distal caudal vertebra is also higher than long (l/h is about 0.76, based on fig. 4H) and is larger than the centrum of MCD-7127 according to the scales in figure 4 of Prieto-Márquez et al. (2019). Presence or absence of the facets for the articulation of the chevron cannot be established because the vertebra is figured only in left lateral view, this detail is not mentioned in the description by Prieto-Márquez et al. (2019) and the posteroventral portion of the centrum may be damaged. The basal part of the neural spine is sloping posteriorly at 22°. MCD-7142 is plausibly a mid-caudal vertebra too. These caudal vertebrae differ from those of *T. insularis* in the minor elongation of their centra; also the shape of the neural spine is unlike those of the neural spines of the caudals of *T. insularis*.

Level 3 of the Blasi locality of the Tremp Syncline near Arèn (Aragòn, NE Spain), base of the Tremp Formation, late Maastrichtian in age (upper part of magnetochron 30n; Pereda-Suberbiola et al. 2009), yielded relatively complete remains of at least 38 caudal vertebrae of hadrosaurids (Cruzado-Caballero 2012, suppl. 9.4, tab. XIII; many inventory numbers are repeated in this list) plus those referred to the lambeosaurine *Arenysaurus ardevoli*.

According to Cruzado-Caballero (2012), the type material of *A. ardevoli* includes 14 associated caudal vertebrae with chevrons (MPZ2006/20; Cruzado-Caballero 2012: fig. 4.90; Fig. 13, partim), a pathological caudal vertebra (MPZ2004/480), 31 other isolated caudals and 13 isolated chevrons (see Cruzado-Caballero 2012: 180-181 for the museum inventory numbers), but the 31 isolated caudals are referred to an indeterminate lambeosaurine in the same work (Cruzado-Caballero 2012: suppl. 9.4, tab. XIII). In the paratype material of *A. ardevoli*, Pereda-Suberbiola et al. (2009) included only the pathological vertebra, the 14 associated caudal vertebrae with chevrons (MPZ2006/20), two other caudal vertebrae (MPZ2008/272 and 313) and two haemal arches (MPZ2008/314 and 330). All these *A. ardevoli* specimens were supposed to belong to a single individual (Pereda-Suberbiola et al. 2009). The vertebral association MPZ2006/20 includes the last four proximal caudals and the first nine or ten mid-caudals, if their relationship is the original one and not an artefact of restoration. The pleurapophysis of the pathologic vertebra MPZ2004/480 is solely a knob ("It has a small transverse process in the posterodorsal part", Canudo et al. 2005: 11), therefore the vertebra is one of the last proximal caudals. The centra of the other proximal vertebrae are much higher than long (l/h ranges 0.52-0.55; Cruzado-Caballero 2012: suppl. 9.4, tab. XIII), bear facets for the haemal arches and their articular facets are hexagonal and flat (Cruzado-Caballero 2012). In lateral view, the neural spines of these proximal caudals are ribbon-like, tall, nearly straight, and slightly inclined backward (Cruzado-Caballero 2012: fig. 4.91). All of the pleurapophyses appear to be broken. The mid-caudal vertebrae of MPZ2006/20 possess centra that are higher than long (l/h at mid-centrum is 0.94 in BLA3/10; Fig. 13) and their neural spines slope backward (this slope is 45° in BLA3/10). The centra bear anterior and posterior articular facets for

Fig. 13 - MPZ2006/20, 14 associated caudal vertebrae of *Arenysaurus ardevoli*, base of the Tremp Formation, upper Maastrichtian, Blasi 3 level, Spain. The posterior segment with the first seven mid-caudal vertebrae. The scale bar equals 50 mm.

the chevrons borne by processes that are equally developed. The postzygapophyses are posterior to the posterior margin of the centrum. In lateral view, the neural spines are recurved and gradually flare apically. They are transversely thick apically and somewhat club-shaped. The cross-section of the basal part of the spine is sub-circular. This is evident in the pathological vertebra MPZ2004/480, which is morphologically like the mid-caudals although it has a hint of a pleurapophysis.

All of the 12 chevrons referred to *A. ardevoli* by Cruzado-Caballero (2012: 203-204) have long, ribbon-like haemal spines that are laterally flattened, have an elliptical cross-section and lack a distal expansion and anteroposterior processes. The only figured haemal arch (BLA3/327; Cruzado-Caballero 2012: fig. 4.97) has a recurved haemal spine and is unexpanded distally, resembling the chevron MCD-4880 from the Basturs Poble bonebed (SI, Fig. 5E-F).

The caudal vertebrae referred to *A. ardevoli* differ from those of *T. insularis* in the minor elongation of their centra, shape and size of the neural spines and shape of the chevrons. The mid-caudal vertebrae differ also from those from the Basturs Poble bonebed in the higher curvature, higher robustness and thicker apical part of the neural spines (compare Figs. 12E-H and 13; apically thick and club-shaped neural spines have not been found in the Basturs Poble bonebed; per. obs.). This supports that the specimens from Basturs Poble bonebed belong to a lambeosaurine distinct from *A. ardevoli* (see Fondevilla et al. 2018), in agreement with the different ages of the two sites.

A sample of 11 partially preserved and isolated proximal and mid-caudal vertebrae from Blasi 3 are summarily described by Cruzado-Caballero (2012; see p. 103 for the inventory numbers) and referred to an indeterminate hadrosaurid. Unfortunately, only a few of them have been figured. The centra of the proximal elements are higher than long (Cruzado-Caballero 2012: 103; suppl. 9.4, tab. XIII). The only nearly complete specimen (the proximal caudal BLA3/212d, Cruzado-Caballero 2012: fig. 4.13A-B) has l/h = 0.59. Its damaged pleurapophyses are long, dorsoventrally flattened but thick proximally and slightly arched dorsally. In lateral view, the neural spine is straight with anterior and posterior margins that slightly diverge apically, and has a posterior slope at 33°. There is no ‘neck’ at the base of the neural spine and no transverse thickening apically. Unfortunately, ventral and dorsal views of this vertebra have not been published. BLA3/50 (Cruzado-Caballero 2012: fig. 4.13C-D;

it bears the same number as one of the caudals referred to *Arenysaurus ardevoli*) is a mid-caudal vertebra, as indicated by the absence of the pleurapophyses and presence of posterior facets for the chevron. The damaged centrum is higher than long (Cruzado-Caballero 2012: suppl. 9.4, tab. XIII). The segment of the neural arch between the pedicels and the postzygapophyses is long and nearly horizontal, so that the postzygapophyses are located well beyond the posterior end of the centrum, like in the mid-caudal MCD-4854 from Basturs Poble locality (Fig. 12E).

Ten fragmentary and isolated chevrons are reported from the Blasi 3 hadrosaurid sample (see Cruzado-Caballero 2012: 99 for the inventory numbers). According to Cruzado-Caballero (2012: 107), they have laterally flattened haemal spines. The only figured chevron of this sample (BLA3/327) is referred to Hadrosauridae indet. in Cruzado-Caballero (2012: fig. 4.17) but is referred to *A. ardevoli* in fig. 4.97 of the same work. Comparison between these chevrons and those of *T. insularis* is impossible, but it is unlikely that the Spanish specimens are like those of the Italian taxon, otherwise it would have noticed by Cruzado-Caballero (2012).

A sample of 26 among the isolated hadrosaurid caudal vertebrae from Blasi 3 listed in Cruzado-Caballero (2012: suppl. 9.4, tab. XIII) includes five proximal caudals, at least 13 mid-caudals and at least three distal caudals. Centra range 63-40.5 mm in length and are all higher than long (l/h ranges 0.48-0.99), except the centrum of the mid-caudal vertebra MPZ2008/310 (l/h = 1.11) and that of the distal caudal vertebra BLA3/231 (l/h = 1.15) which is referred to an indeterminate lambeosaurine. Two other isolated vertebrae, which are reported as proximal caudals of an indeterminate lambeosaurine by Cruzado-Caballero (2012; MPZ2008/275 and MPZ2008/276), have facets for the haemal arches, thus they are not the first vertebrae of the tail; their centra are much higher than long (l/h is 0.58 and 0.55, respectively; Cruzado-Caballero 2012: suppl. 9.4, tab. XIII).

All of these caudals of indeterminate hadrosaurids from Blasi 3 differ from those of *T. insularis* in the minor elongation of the centra, shape and size of the neural spines and shape of the pleurapophyses, when preserved.

France

The upper Maastrichtian dinosaur-bearing sites of southern France have yielded several isolated caudal vertebrae of hadrosaurids (Laurent 2003; Dalla Vecchia 2014), but only those from the Lestaillats 1 locality (Plagne Anticline, Haute Garonne, Petites Pyrénées) are adequately preserved for comparison. This site, which is located in the early late Maastrichtian Marnes de Lestaillats (Laurent 2003: fig.7), yielded three complete proximal caudals (MDE-Les1-4, 5 and 20). They were referred to indeterminate “hadrosaurids” by Laurent (2003). Their centra are higher than long with nearly flat articular facets and bear long pleurapophyses; their neural spines are tall and ribbon- shaped in lateral view (Laurent 2003; Fig. 14). These caudals differ in details, suggesting that they are from different positions of the proximal part of the tail.

The centrum of MDE-Les1-5 (Fig. 14A-B) is rather anteroposteriorly short (l/h = 0.63), has sub-circular articular facets, and no facets for the haemal arch. The pleurapophyses are directed laterally, taper distally and have a robust, wing-like dorsoproximal lamina like the vertebra MCD-8638 from the Spanish Els Nerets locality. Similar pleurapophyses occur also in a vertebra of the holotype of *Hypacrosaurus altispinus* that Brown (1913b: figs. 1 and 3) identified as the first caudal. Therefore, MDE-Les1-5 is probably the first caudal, as noticed by Laurent (2003). Apically, the neural spine (which is deformed and was restored) is slightly recurved, does not flare anteroposteriorly and is not much thickened transversely; it slopes posteriorly at 18.5° and its lateral sides show basoapical striae.

The centrum of MDE-Les1-4 (Fig. 14C-E) has also sub-circular articular facets, but it presents posteroventral processes bearing the articular facets for the haemal arch and no anterior processes and articular facets. The centrum is markedly higher than long (l/h = 0.75). The pleurapophyses are rod-like, anteroposteriorly narrow (finger-like), slightly flattened dorsoventrally and directed lateroposteriorly and lateroventrally. The pleurapophyses do not taper, do not expand distally and do not have a constriction in the middle. The neural spine is straight, ribbon-like with parallel anterior and posterior margins and does not expand apically in lateral view; its posterior slope is 18°. The neural spine is laterally flattened and not club-shaped (it is only slightly transversely thickened apically). A prespinal lamina is developed in the anterior basal half of the spine. There is a hint of a ‘neck’ in the posterior basal portion of the spine just above the postzygapophysis, but it is much less marked than in

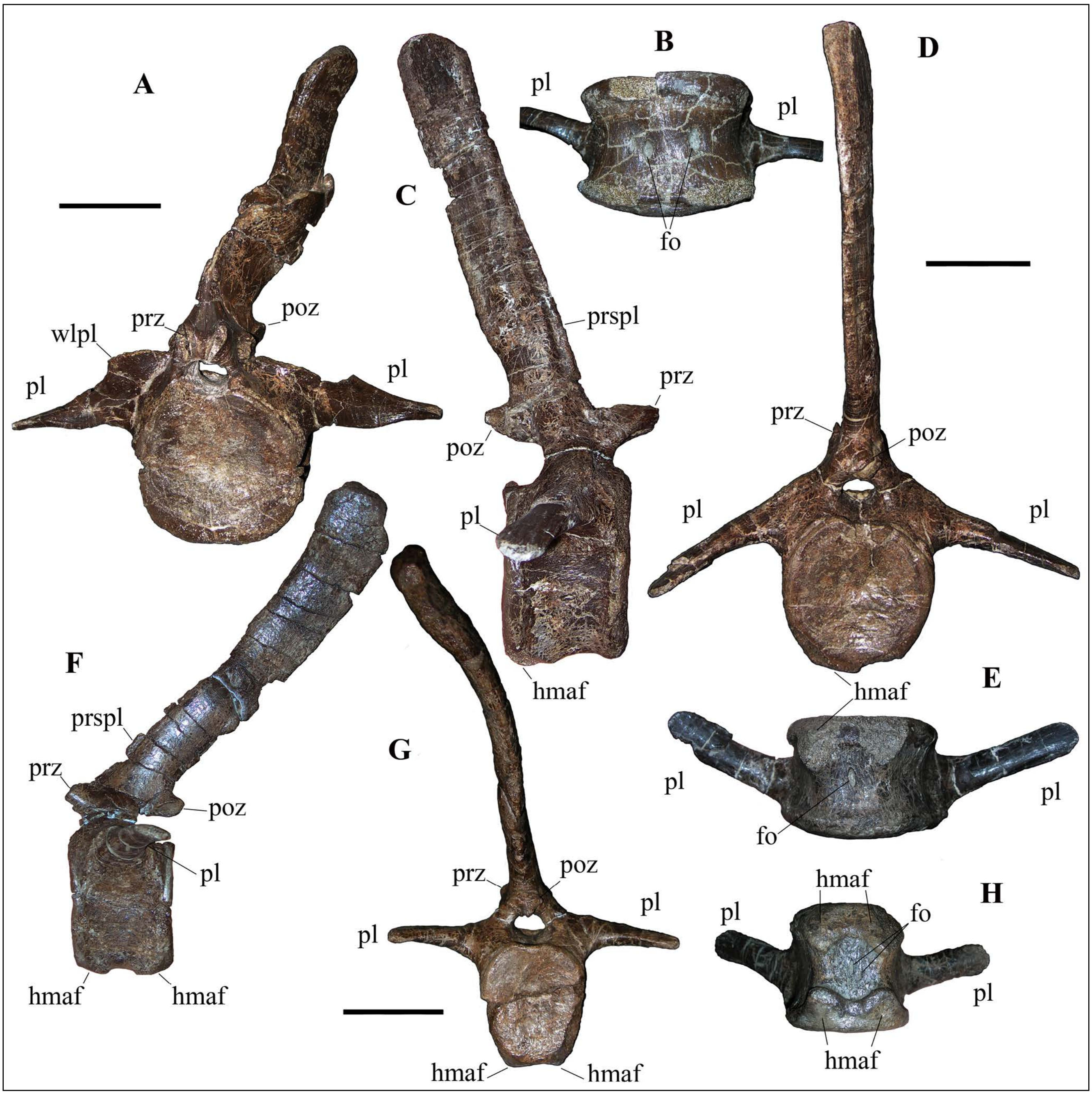

Fig. 14 - The caudal vertebrae of an indeterminate hadrosaurid (probably a lambeosaurine) from the upper Maastrichtian Lestaillats 1 locality, France. A-B) MDE-Les1-5, first caudal vertebra, anterior (A) and ventral (B) views; C-E) MDE-Les1-4, probably the first chevron-bearing caudal vertebra, right lateral (C), posterior (D) and ventral (E) views; F-H) MDE-Les1-20, from a middle position in the proximal segment of the tail, left lateral (F), posterior (G) and ventral (H) views. Abbreviations: fo, nutritive foramen; hmaf, articular facet for the haemal arch; pl, pleurapophysis; poz, postzygapophysis; prspl, prespinal lamina; prz, prezygapophysis; wlpl, wing-like proximodorsal lamina of the pleurapophysis. The scale bars equal 50 mm.

T. insularis and in the two proximal caudals from Transylvania (NHMUK PV R. 4915 and NHMUK PV R.4973). The height of the neural spine is about 2.2 times the centrum height. The shape of the articular facets of the centrum, the length of the pleurapophyses, the shape and low posterior slope of the neural spine and the development of the articular structures for the chevron suggest that MDE-Les1-4 is the first chevron-bearing caudal vertebra of the tail.

MDE-Les1-20 (Fig. 14F-H) has articular facets of the centrum that are much higher than wide and well-developed anterior and posterior articular structures for the chevrons. The centrum is higher than long (l/h = 0.82). The pleurapophyses are like those of MDE-Les1-4, but are directed laterally instead of lateroventrally and are proportionally shorter. The neural spine is more inclined posteriorly (38°) than that of MDE-Les1-4. In its apical half, the neural spine slightly flares anteroposteriorly and is recurved; it is flattened laterally, but its apical part is thickened transversely. The height of the neural spine is about 2.5 times the centrum height. This caudal vertebra is from a middle position in the proximal segment of the tail.

The caudals from Lestaillats 1 are relatively small-sized and the presence of the neurocentral suture and large nutritive foramina on the ventral side of the centra (Fig. 14B, E and H) suggests that they belong to immature individuals.

The associated ischia (MDE-Les1-1, 2, and 19) have slender and sigmoid shafts that resemble the shafts of the ischia of SC 57247 (Laurent 2003: pl. 40). However, all of the Lestaillats 1 vertebrae are rather different from those of *T. insularis* in the l/h ratios of the centra, shape of the pleurapophyses, relative size and morphology of the neural spines and probably also in the position within the caudal vertebral column of the first chevron-bearing vertebra (i.e., the first chevron-bearing vertebra was much more proximal in the French taxon than in the Italian one). Furthermore, the articular facets of the zygapophyses appear to be less inclined than those of *T. insularis* (i.e., the articular facets are not nearly vertical in the French taxon; see Laurent 2003).

Belgium and the Netherlands

A few isolated caudal vertebrae of hadrosaurid dinosaurs come from the marine Maastricht Formation ("Chalk"; late Maastrichtian in age) of the Limburg (Belgium and the Netherlands). Two caudal vertebrae, which are deposited at the IRSNB, were described and figured by Dollo (1883), although measurements and localities of provenance are not given in that paper. The neurocentral suture is still visible in both vertebrae, indicating that they belong to immature individuals (but see the comment by Buffetaut 2009: 3). One specimen is the right half of an amphicoelous centrum with the base of the right pedicel of the neural arch and the proximal part of the right pleurapophysis (Dollo 1883: figs. 1-2). The centrum appears to be about as high as long or slightly higher than long, if it is ventrally complete. It is a proximal vertebra that Dollo (1883) considered as the first or the second caudal because it appeared to lack the articular facets for the haemal arch.

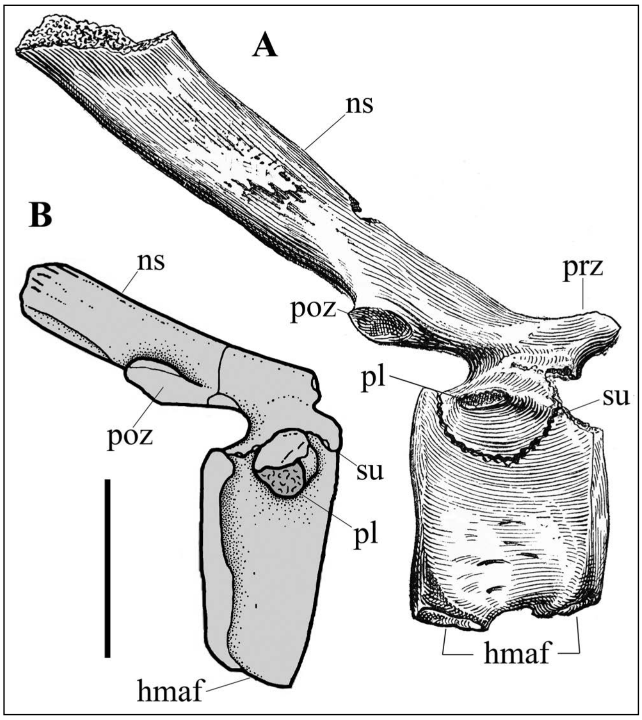

Fig. 15 - The proximal caudal vertebrae of indeterminate hadrosaurids from the upper Maastrichtian of Limburg (Belgium and the Netherlands). A) specimen stored at IRSNB (without number) and figured by Dollo (1883: fig. 5); B) MB.R.4450. They are shown in right lateral view. Abbreviations: hmaf, articular facet for the haemal arch; ns, neural spine; pl, pleurapophysis; poz, postzygapophysis; prz, prezygapophysis; su, neurocentral suture. A is from Dollo (1883), modified; B is redrawn from Buffetaut (2009). Scale bar in B equals 50 mm. The size of the IRSNB vertebra was not reported in Dollo (1883).

The other specimen is a nearly complete proximal caudal (Fig. 15A). The amphicoelous centrum has both anterior and posterior articular facets for the haemal arches and is as long as high (l/h = 1.00). The pleurapophyses project from the basal part of the pedicels of the neural arch, which expand ventrally on the lateral side of the centrum, as it is shown by the neurocentral suture. The distally incomplete pleurapophysis is dorsoventrally flattened (Dollo 1883: fig. 6) and has an elliptical cross-section. The apically incomplete neural spine is nearly straight, laterally flattened, inclined posteriorly at ca. 50° and flares apicad in lateral view, but its extremity is not much thickened transversely.

A partial proximal caudal (MB.R.4450; Fig. 15B) from the Dutch part of Limburg was described and figured by Buffetaut (2009: fig. 1). Its centrum is incomplete, but it was clearly higher than long when entire and its posterior articular facet is concave. The only preserved facet for the haemal arch is posterior; this facet is wide and deep, but not set on a projecting process as in the IRSNB vertebra. The broken pleurapophysis has a sub-circular cross section. The neurocentral suture is open and occurs dorsal to the pleurapophysis (i.e., the pleurapophysis projects from the centrum, unlike the IRSNB vertebra). The neural spine is very inclined backward (the basal preserved part slopes at 62°) and is slightly flattened laterally, with an elliptical cross-section and nearly parallel anterior and posterior margins. The postzygapophyses are posterior to the posterior margin of the centrum and their articular facets are inclined at about 45°. The segment of the neural arch from the top of the pedicels to the postzygapophyses is nearly horizontal. The l/h ratio, morphology of the facet for the haemal arch and the robust pleurapophysis would suggest it is from a more proximal position than the IRSNB vertebra, but the high posterior slope and slenderness of the neural spine is in contrast with this interpretation. Furthermore, the cross-section of the pleurapophysis is different in the two vertebrae and the pleurapophysis of MB.R.4450 is placed on the centrum instead of the neural arch as in the IRSNB vertebra, although the position of the pleurapophysis with respect to the dorsal margin of the centrum is the same. This may indicate that MB.R.4450 and the IRSNB vertebra belonged to two distinct taxa.

The three Limburg vertebrae are rather unlike the proximal caudals of *T. insularis* in the l/h ratios of the centra, shape of the pleurapophyses, and size and morphology of the neural spines.

Germany

A small (ca. 25 mm long) and amphicoelous vertebral centrum from the marine Gerhartsreiter Schichten of southern Germany (Maastrichtian in age; Wellnhofer 1994; López-Martínez et al. 2001) was reported as a "sub-terminal caudal vertebra" of an indeterminate hadrosaurid by Wellnhofer (1994: 228). It lacks haemapophyseal facets and belongs to a distal caudal vertebra. Unlike the centra of *T. insularis*, the German specimen is higher than long (l/h is ca. 0.80; Wellnhofer 1994: fig. 5I-L). It is associated with other bones from a single, small-sized hadrosaur, including a neural arch that was identified as the "neural arch of a proximal caudal vertebra" (Wellnhofer 1994: 229). However, the high position of the "transverse process" (Wellnhofer 1994: 229) on the neural arch suggests it belongs to a dorsal vertebra.

The life and burial environment of *Tethyshadros insularis*

Like the other hadrosauroids from the uppermost Cretaceous of Europe, *T. insularis* was an insular dweller (Fig. 9), but it lived in a peculiar environment. Unlike hadrosauroids from Romania, Spain, France and probably also Belgium-the Netherlands and Germany, *T. insularis* lived on the emergent part of a shallow water carbonate platform, which was a karst like that existing today in the same area (the Carso/Kras Plateau of Italy and Slovenia, from which the Anglo-Saxon term "karst" originates), but under a tropical or sub-tropical climate, because the region was at a latitude of about 30°N during the latest Cretaceous (Philip et al. 2000). Thin bauxite levels found just below the Liburnian Formation and coal seams in the lower half of this formation (Jurkovšek et al. 1996; Venturini et al. 2008) may indicate deposition under a relatively humid climate. A modern analogous could be the tabular limestone platform of the Yucatán Peninsula, which is an emergent carbonate plateau within the Central American tropical belt (Finch 1965). In karsts, surface streams are rare because runoff is directed underground through openings and fractures in the limestone. Because the water flow is essentially underground into carbonate dissolution cavities, surface water supply is limited.

At the Villaggio del Pescatore site, dinosaur remains were found in a ~10 m-thick body of black, well-bedded and mostly thinly laminated limestone (hereafter reported as laminites) (Tarlao et al. 1994; Palci 2003; Dalla Vecchia 2008). The remains of the other European hadrosauroids are usually preserved into terrigenous fluvial deposits and palaeosoils or, less frequently, into sediments deposited in open marine settings (Therrien 2005; Dalla Vecchia 2006, 2014). The body of laminites originated into a depression within older shallow marine limestone with karstified sides and bottom, and is surrounded by breccia bodies (Tarlao et al. 1994; Palci 2003); the main dimension of its cropping out portion is 80 m (Palci 2003).

The collected dinosaur sample is represented by remains of at least six distinct individuals, all referable to *T. insularis* and all with a modest body size as the holotype (Dalla Vecchia 2009c). *T. insularis* fossils are represented by isolated scattered bones at the base of the laminites (most of these bones partially cropped out of the rock layer and were not collected during the field work), while articulated skeletons occur in the middle-upper part of the lithosome (Dalla Vecchia 2008, fig. 1; pers. obs.).

The laminites have yielded also remains of small crocodyliforms (including the holotype and paratype of the new species *Acynodon adriaticus*; Delfino et al. 2008); a single pterosaur bone (Dalla Vecchia 2018); at least 120 small fishes (2-5 cm long; pers.obs.), apparently monospecific; a few fragmentary fishes of larger size (less than 20 cm, anyway; pers. obs.); several crustaceans (a few large shrimps and many small shrimp-like crustaceans concentrated on a few bed surfaces; pers.obs.); some small coprolites; and a few and poorly preserved plant remains including a conifer branch (Dalla Vecchia 2008). According to Palci (2003), foraminifers are represented by a few miliolids and rotaliids, which are organisms that have been reported also from brackish environments. Remains of freshwater plants (characeans) also occur. The $\delta^{13}C$ and $\delta^{18}O$ isotopic values measured from samples taken in the laminites and in the surrounding breccias are always negative, thus they do not support a marine origin of the sediments (Palci 2003).

Circulation was restricted in the water-filled depression, developing fluctuating dysoxic to anoxic conditions allowing the development of an oligotypical (monospecific?) small fish community and the presence of a few other organisms. The good state of anatomical articulation of the two dinosaur specimens considered in this paper suggests a very limited transport after death and an undisturbed deposition in a low energy protective environment. Since lamination is sub-millimetric, the good state of preservation of the specimens cannot be due to rapid burial under a thick sediment mantle, but to the peculiar conditions of the water at the bottom.

Although the depression has been considered basically of tectonic origin (Tarlao et al. 1994; Palci 2003), an important role in its formation was probably played also by the carbonate dissolution, because of the karst setting and by comparison with modern analogues. The depression could have been a cenote or a similar karst structure, i.e. a vertical-walled sink-hole like those characteristic of the present day Yucatán plateau (Finch 1965) and emergent parts of carbonate platform islands in the tropical belt (the latter are often reported in the English literature as blue holes). Cenotes can be the main source of fresh water on the surface during the dry season. Water supply is a problem for large tetrapods living in a karst, mainly during the dry season, because there is no superficial water drainage as waters flow or stay in the fissures and cavities produced by carbonate dissolution inside the rock body. A cenote could also attract animals for this reason. Cenotes are traps for terrestrial tetrapods because of their vertical walls that prevent to go out once fallen into and because of the thick vegetation surrounding and concealing them. Subfossil remains of crocodilians, tortoises, birds and a caviomorph rodent dated to 3900-2500 years BP have been collected in the peat formed at bottom of a blue hole with anoxic water in the Abaco island of The Bahamas (Steadman et al. 2007).

The perfectly articulated skeleton of the holotype of *T. insularis* could be the remains of an individual who had fallen, drowned and deposited at the bottom of a cenote-like sink-hole developed into the Adriatic carbonate platform. Preservation was favoured by dysoxic to anoxic conditions of the bottom waters due to their stagnation. The unusual folding of the tail of SC 57247 was caused by the slump fold of the unstable fine carbonate sediment partially filling the sinkhole, covering the steep and coarser talus deposits and sometimes mixing with them. Evidences of synsedimentary faulting and displacement of the sediment involving the skeletons occur also in the holotype (Fig. 1) and specimens SC 57022 (Fig. 16C-D) and SC 57026.

DISCUSSION

Gracile and robust morphs

The holotype and SC 57247 share the same morphology of the neural spines in the caudals, both possess proximal caudal centra that are longer than high, their first chevron is very distal in the tail and their ischia are extremely long and slender. Furthermore, they come from the same outcrop and SC 57247 was preserved only a few metres stratigraphically above the holotype (Dalla Vecchia 2008: fig. 1) in the same body of laminites, corresponding to a few thousand years of deposition at maximum, if Arbulla et al. (2006) are correct in their interpretation of the cyclicity of the deposition. Therefore, it is assumed that the holotype and SC 57247 belong to the same species (Dalla Vecchia 2009c).

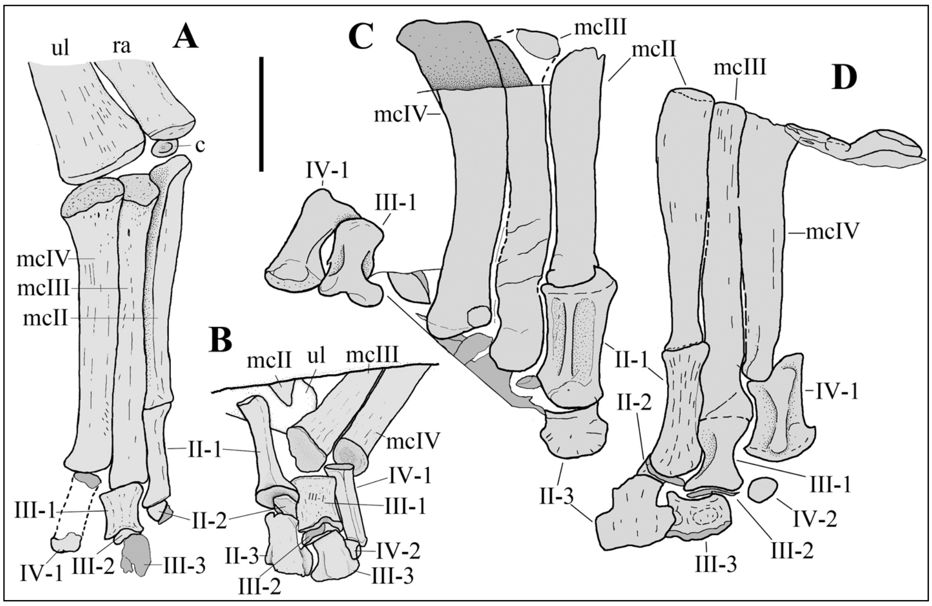

Fig. 16 - Mani of *Tethyshadros insularis* and their different robustness. A) Right manus of SC 57021 (holotype); B) left manus of SC 57021 (holotype); C) left manus of SC 57022; D) right manus of SC 57022. Abbreviations: II-1 to 3, phalanges 1 to 3 of digit II; III-1 to 3, phalanges 1 to 3 of digit III; IV-1 to 2, phalanges 1 to 2 of digit IV; c, carpal; mcII-IV, metacarpals II-IV; ra, radius; ul, ulna. The scale bars equal 50 mm.

SC 57247 is not significantly larger than the holotype, as it is evident from the similar lengths of the skulls and proximal caudal vertebral centra, but it is more robust (Dalla Vecchia 2009c: 1102). The specimens SC 57247 and SC 57022 (two mani and right radius and ulna; Fig. 16C-D) belong to a robust morph, while the holotype belong to a gracile morph (Dalla Vecchia 2009c). The presence of associate gracile and robust individuals within a sample of a dinosaur species is not uncommon: it is reported in the basal sauropodomorphs *Plateosaurus engelhardti* (see Galton 1997) and *Thecodontosaurus antiquus* (see Benton et al. 2000), the theropods *Coelophysis bauri* (see Colbert 1990; Rinehart et al. 2001), *Syntarsus rhodesiensis* (see Raath 1990) and *Tyrannosaurus rex* (see Carpenter 1990; Larson 2008), the basal iguanodontian *Zalmoxes robustus* (see Weishampel et al. 2003) and an indeterminate lambeosaurine (see Fondevilla et al. 2018). The presence of gracile and robust individuals within a sample of supposedly adult members of a non-avian dinosaur species has often been related to sexual dimorphism (Raath 1990; Carpenter 1990; Galton 1997; Larson 2008), but without definitive evidence (Mallon 2017). Anyway, size dimorphism is widespread throughout extant animal populations (Fairbairn et al. 2007). Most of the extant animal species are sexually dimorphic rather than monomorphic (Andersson 1994; Isles 2009), including birds (Lezana et al. 2000; Campos et al. 2005; Isles 2009; Delgado Castro et al. 2013) and crocodiles (Lang 1987; Allsteadt & Lang 1995; Larson 2008; Platt et al. 2009; Isles 2009). Therefore, the presence of sexual dimorphism in *T. insularis* would not be unexpected. The specimens of *T. insularis* lived in the same geographic spot and can be considered as coeval for the standards of the geological time, thus it is improbable that their morphological differences may be due to geographic and temporal factors (Mallon 2017).

Different robustness may be indicative of a different ontogenetic stage, but the robust SC 57247 shows more macro-evidences of osteological immaturity than the gracile holotype. In fact, although the sacral vertebrae of SC 57247 are fused into a synsacrum and the sacral ribs are fused to the transverse processes of the sacral vertebrae, the ilia are unfused to the synsacrum. If not an artefact of preparation, the first caudal ribs were unfused to their transverse processes. Also some skull bones are evidently unfused each other in SC 57247. Only a skeletochronological age determination of the two specimens, which has not yet been attempted, could shed light on this aspect.

The shape of the haemapophyses is unlike in the two *T. insularis* specimens. If this is a real feature and not an artefact of preparation, it is, together with the different robustness of the centra and possibly the shape of the pleurapophyses of the first seven caudal vertebrae, the most striking difference between the two tails. Romer (1956: 267) considered the variation in the position of the first haemapophysis in living turtles and crocodilians as related to sex. Based on the presumed different position of the first haemapophysis in males and females of *Alligator mississippiensis*, Larson & Frey (1992) and Larson (1994) had presumed the sex of specimens of the theropod *Tyrannosaurus rex*. Later, Brochu (2003) and Erickson et al. (2005) have shown that the position of the first haemal arch is not related to sex in *Alligator mississippiensis*. Persons et al. (2015) have considered as a sexual feature the different shape and robustness of the first haemal arches of two specimens of the oviraptorid theropod *Khaan mckennai*. However, only the first chevrons are differently robust in the two specimens of *K. mckennai*, whereas all of the preserved chevrons are different in the two specimens of *T. insularis*. Furthermore, Persons et al. (2015) related the purported sexual differences in the haemal arches of *K. mckennai* to tail-feather displays in courtship behavior. As the tail of *T. insularis* was plausibly featherless, analogy between the condition in *T. insularis* and *K. mckennai* is not possible. However, this does not exclude that the differences in the tails of the two specimens of *T. insularis* are due to sexual dimorphism.

These morphological differences might also be related to the possible condition of *T. insularis* as a r-strategist species (see Pianka 1970 for a definition) in an insular setting, because insular r-strategist tetrapods are supposed to show wide intraspecific morphological variability (Raia et al. 2003: 304).

The *T. insularis* sample is still limited, but it could be increased in the future because more specimens can be extracted from the Villaggio del Pescatore site. Furthermore, the ontogenetic influence on the morphological variability will hopefully be tested by the skeletochronological age determination of the already available specimens. This will shed more light on the possible dimorphism of *T. insularis*, hopefully allowing establishing whether it is sexual or not.

Tethyshadros and the other hadrosauroids of the European archipelago

Tethyshadros insularis is, with the taxon from Romania, the only taxon in the sample of European latest Cretaceous hadrosauroids to have proximal caudal centra that are longer than high. Proximal caudal centra are usually higher than long also in the continental hadrosauroids (e.g., Parks 1920; Lull & Wright 1942; Norman 1986, 2002, 2004; Godefroit et al. 1998; Horner et al. 2004). The two caudal vertebrae from Romania are the most similar to those of *T. insularis* within this sample. This is in agreement with the close phylogenetic relationship of *T. insularis* and *Telmatosaurus transsylvanicus* found by the phylogenetic analysis of Dalla Vecchia (2009c), Xing et al. (2012, 2014) and Wang et al. (2015) and supports the belonging of those caudals to the Romanian taxon. *T. insularis* and *Telmatosaurus transsylvanicus* have possibly a similar age and lived in palaeogeographically close islands (see Dalla Vecchia 2009c and Csiki-Sava et al. 2015; Fig. 9).

However, the caudals from Transylvania differ from the proximal caudals of the holotype of *T. insularis* in the minor elongation of the centrum, neural spines that are less expanded apically in lateral view and pleurapophyses that are not tongue-like or petaloid. The caudal vertebrae with upright and meat cleaver-shaped neural spines in lateral view are vertebrae 1 to 5 in *T. insularis* and they do not have haemapophyseal processes, because chevrons start from caudal 7 or 8; chevron-bearing proximal caudals of *T. insularis* have fan-shaped spines with an higher posterior slope than that of the only complete Transylvanian caudal. This suggests that the chevrons started in a more proximal position of the tail in the Transylvanian taxon with respect to *T. insularis*, as it is usual in hadrosauroids.

All of the hadrosauroid vertebrae from the Maastrichtian localities of the Conca Dellà and Blasi (Spain), France, Belgium and the Netherlands differ from *T. insularis* caudals also in the shape of the neural spines and pleurapophyses. Furthermore, the haemal arches from Spain are all of the simple finger-like type. The morphology of the proximal caudal vertebra from type material of *P. isonensis* suggests that the first chevrons was placed in the first caudals in this taxon, unlike *T. insularis* and like all others hadrosauroids; this appears to be the case also for the caudal vertebrae from France.

The peculiarity of *T. insularis*' tail cannot be explained as a consequence of insularity alone, because all of the hadrosauroids from the European archipelago were insular dwellers.

Implications of the tail morphology of *Tethyshadros insularis*

Unlike other hadrosauroid dinosaurs, the diagnosis of *T. insularis* includes seven apomorphic features related to the caudal vertebral column (Dalla Vecchia 2009c: 1100 and 1102). Comparison with the hadrosauroid caudal vertebrae from the uppermost Cretaceous of Europe reported above supports the peculiarity of those features.

The caudal series of *T. insularis* was modified from the relatively conservative hadrosauroid tail bauplan for some particular functions. Theses functions may be an important factor in the successful adaptation of this dinosaur to an unusual mode of life, as it has been hypothesized for non-avian theropods (Ostrom 1969). Atypical traits may reflect an adaptation to the peculiar habitat of *T. insularis* in a karst island.

Skeletal features of the tail are strictly connected with tail musculature in living reptiles and are supposed to be such also in extinct non-avian dinosaurs by inference (Romer 1923, 1927; Frey et al. 1989; Gatesy 1990; Arbour 2009; Mallison 2011; Persons & Currie 2011a, 2014; Otero et al. 2012; Ibiricu et al. 2014). However, the relationships between tail skeleton and tail muscles and even the presence of some tail muscles are taxonomically variable in extant reptiles (e.g., Frey et al. 1989; Gatesy 1990; Wilhite 2003; Schwarz-Wings et al. 2009; Arbour 2009; Mallison 2011; Persons & Currie 2011a; Otero et al. 2010; Ibiricu et al. 2014) and the reconstructions of the tail musculature in non-avian dinosaurs are consequently somewhat different to each other. Anyway, hypotheses about the relationships between the peculiar skeletal features in the tail of *T. insularis* and their related soft tissues can be formulated only by inference from extant reptiles and by inferences made on other non-avian dinosaurs. Speculation on the adaptive importance of such features is also possible by inference based on the functional morphology and physiology of extant archosaurs and other reptiles.

Elongation of the vertebral centra. As in the other hadrosauroids, the centra become more elongated moving distally along the tail in *T. insularis*. However, starting from an condition of centra longer than high already in the first caudal vertebrae (SI, Tab. 1), the mid-caudal vertebrae of the holotype of *T. insularis* are comparatively much more elongated than in other hadrosauroids. This peculiar elongation of the caudal centra has the following consequences: 1) number of caudal vertebrae being equal, it makes for a longer tail; 2) location of the first haemapophysis being equal, it contributes to shift posteriorly its position; 3) number of proximal caudal vertebrae being equal, it shifts posteriorly the position of the last pleurapophyses. The elongation of the posterior proximal and mid-caudal centra of the holotype of *T. insularis* is comparable to that of the corresponding caudal centra of *Tenontosaurus tilletti* (see Forster 1990). The long tail, which accounts for 67% of the total body length, is considered a diagnostic feature of this North American taxon (Forster 1990: 274; Norman 2004), but its functional morphology has never been investigated.

The elongation of the mid-caudal centra, as well as, plausibly, of the distal centra, and the lowering of the corresponding chevrons and neural spines, made the distal half of the holotype tail whip-like, with a marked shallowing just after the proximal segment (Fig. 8).

The tail of the robust individual (SC 57247) has relatively less elongated proximal caudal centra, suggesting that the elongation of these centra is somewhat intraspecifically variable.

Centra of caudal vertebrae 23 to 33 with the shape of amphicoelous semicylinders. The centra of vertebrae 23 to 33 are “platycoelous” (= amphiplatyan) and “hexagonal in cross section” in *Tenontosaurus tilletti* (Forster 1990: 278). In *Iguanodon bernissartensis* (see Norman 1980: 43) and *Mantellisaurus atherfieldensis* (see Norman 1986: 310), these centra are also amphiplatyan and “hexagonal cylinders” i.e., they have a hexagonal cross-section. Caudal centra are amphiplatyan in the non-hadrosaurid hadrosauroid *Bactrosaurus johnsoni* and mid-tail centra have a hexagonal cross-section (Godefroit et al. 1998). The articular facets of the posterior mid-caudal centra of the non-hadrosaurid hadrosauroid *Eolambia caroljonesa* are slightly concave and hexagonal (McDonald et al. 2012a, 2017). Caudal centra 23-35 of the non-hadrosaurid hadrosauroid *Nanyangosaurus zhugeii* are “platycoelous” and have “regular hexagonal...outlines in anterior or posterior view” (Xu et al. 2000: 37-38). In hadrosaurids, the “outline” of the caudal centra is hexagonal according to Horner et al. (2004: 453). At least in the saurolophine *Edmontosaurus annectens* (see Sternberg 1926), *Brachylophosaurus canadensis* (see Prieto-Márquez 2001) and *Saurolophus angustirostris* (see Maryánska & Osmólska 1984), mid-caudal centra are amphiplatyan. The description of the articular facets of the centra in the many other hadrosaurid species with preserved mid-caudal vertebrae was omitted in the papers dedicated to their osteology.

The peculiar shape of the mid-caudal centra of the holotype of *T. insularis* had probably a specific function, which is not immediately clear because of the absence of extant analogues.

Number, shape and elevation of the pleurapophyses. In reptiles, "generally the proximal caudals, to the number of half a dozen to a dozen or more, bear fused ribs" (Romer 1956: 268). The holotype of *T. insularis* has at maximum 14 pleurapophyses-bearing (i.e., proximal) caudal vertebrae. The saurolophine hadrosaurid *Edmontosaurus annectens* (see Lull & Wright 1942: 79), *Saurolophus osborni* (see Brown 1913a: 389) and *Brachylophosaurus canadensis* (see Prieto-Márquez 2001: 148), and the non-hadrosaurid hadrosauroid *Nanyangosaurus zhugeii* (see Xu et al. 2000: 188) have 19 proximal caudals. *N. zhugeii* is higher in the phylogenetic tree than *T. insularis* according to McDonald et al. (2012b). A specimen of the saurolophine hadrosaurid *Gryposaurus notabilis* has at least 17 proximal caudals, but its tail is distally incomplete (Parks 1920: 30). Among the lambeosaurine hadrosaurids, *Corythosaurus casuarius* has 15 (Brown 1916: 711) or "anywhere from 13 to 16" (Ostrom 1963: 154) proximal caudals and *Barsboldia sicinskii* has at least 16 (Maryánska & Osmólska 1981: 247). The non-hadrosaurid hadrosauroid *Xuwulong yueluni* has apparently 13 or 14 proximal caudals (You et al. 2001: fig. 2). *X. yueluni* is more basal than *T. insularis* according to McDonald et al. (2012b). *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* have 14 (see Norman 1980: 43) and 15 or 16 (Norman 1986: 310) proximal caudals, respectively. In the dryosaurid *Dryosaurus altus*, the pleurapophyses are present up to caudal 12 (Galton 1981: 280). *Tenontosaurus tilletti* has eight proximal caudals (Forster 1990). The small basal iguanodontian *Gasparinisaura cincosaltensis* has 11 proximal caudals (Coria & Salgado 1996: 448). Therefore, the number of caudals with pleurapophyses appears to be somewhat phylogenetically biased and *T. insularis* retains a plesiomorphically low count. Despite to this, the higher elongation of the centra compensates for the low number of proximal caudals, and the proximal segment of the tail of *T. insularis* is proportionally longer than that of a hadrosaurid.

The pleurapophyses of the first five caudals are tongue-shaped in the holotype (Fig. 5), whereas they appear to be spatula-shaped in SC 57247. Therefore, the shape of the pleurapophyses may be somewhat intraspecifically variable, if this is not an artefact of preparation.

Broad pleurapophyses offer a larger surface for the origin or insertion of the tail musculature than slender pleurapophyses. The epaxial *M. longissismus caudae* (LCA) inserts dorsally on the pleurapophyses in extant crocodilians (Frey 1982; Persons & Currie 2011a; Mallison 2011) and it is supposed to have inserted there also in non-avian dinosaurs (Arbour 2009: fig. 9a-c; Persons & Currie 2011a: fig. 2a-b; Mallison 2011: fig. 4). LCA is supposed to originate from the postacetabular process of ilium in non-avian dinosaurs (Dilkes 2000: 103; Arbour 2009: 7) and to extend along the full length of the tail. The pleurapophyses have a relationship also with the hypaxial *M. caudofemoralis longus* (CFL), which originates from the lateral sides of the haemapophyses and the lateral and ventral sides of the centra of the haemapophyses-bearing vertebrae in extant crocodilians (Ibiricu et al. 2014: tab. 3) and supposedly also in dinosaurs (e.g., Gatesy 1990; Wilhite 2003; Persons & Currie 2011a; Otero et al 2012; Ibiricu et al. 2014). In extant crocodilians, the CFL does not originate from the pleurapophyses (Wilhite 2003: 83; Persons & Currie 2011a: 125) or it does it minimally only in the "first few" pleurapophyses (Ibiricu et al. 2014: 462). Nevertheless and despite the fact that the CFL ends before the disappearance of the pleurapophyses in some extant reptiles (Persons & Currie 2011a), a correlation between the decreasing in size of the pleurapophyses and the distal tapering of the CFL is hypothesized in many reconstructions of the tail musculature of non-avian dinosaurs (Gatesy 1990; Wilhite 2003; Persons & Currie 2011a; Otero et al. 2012; Ibiricu et al. 2014) "because the transverse processes form a "shelf" under which *M. caudofemoralis longus* runs" (Wilhite 2003: 93). Being the CFL dorsally constrained by the pleurapophyses, the position and orientation of these processes are indicative of the dorsal extent of the muscle (Wilhite 2003; Persons & Currie 2011a, 2014). As in the other hadrosauroids, the pleurapophyses of *T. insularis* are not elevated above the centrum, unlike the condition in non-avian theropods, where elevation of the pleurapophyses above the centrum indicates a higher dorsal development of the hypaxial musculature than in hadrosauroids (Persons & Currie 2011a, b, 2014).

Shape and size of the neural spines. Although there appears to be a slight difference in shape among the proximal neural spines in the holotype and SC 57247, the upper part of the spine in lateral view is apomorphically expanded in both of them. As seen above, the neural spines of the proximal caudal vertebrae of *T. insularis* are comparatively much broader anteroposteriorly than those of the other hadrosauroids from the European archipelago. The neural spines are comparatively broader in basal hadrosauroids and more basal iguanodontians (for example, *Iguanodon bernissartensis*; Norman 1980: fig. 47) than in hadrosaurids and became peculiarly taller in the lambeosaurines (Horner et al. 2004). Therefore, the shape and size of the neural spines appear to be somewhat biased phylogenetically. Taller neural spines indicate a higher development of the epaxial musculature and have therefore a functional significance (Schwarz-Wings et al. 2009), which has never been investigated in hadrosauroids.

In the holotype of *T. insularis*, the neural spines are broader in correspondence with the larger and broader pleurapophyses of the chevron-less first proximal vertebrae. Broader neural spines give a wider surface for the origin and insertion of muscles of the epaxial *M. transversospinalis* system (Organ 2006; Arbour 2009: fig. 9; Persons & Currie 2011a: fig. 2; Mallison 2011: fig. 4), which is associated with the ossified tendons (Organ 2006) occurring up to caudal vertebra 20 in the holotype of *T. insularis*.

The anteroposteriorly long apical margin of the neural spines of *T. insularis* suggests the presence of a comparatively long attachment for the *ligamentum supraspinale* (Schwarz-Wings et al. 2009). However, the transversely flattened spines indicate that the diameter of this ligament was reduced.

The comparatively low and broad proximal neural spines of *T. insularis* might be better suited to avoid injuries during mating than the taller and slender spines of the hadrosaurids (Rothschild 1994); in that case, the spinal shape might be sexually dimorphic.

Shape and size of the haemal arches. According to Horner et al. (2004: 453), the first five haemal arches are more inclined posteriorly than the following ones and often touch each other in hadrosaurids, while, according to Lull & Wright (1942: 81), “the anterior three or four chevrons are smaller and are bent strongly backward to clear the essential passages which must have lain above the ischia”. For Romer (1956: 273), “in hadrosaurs... the first few chevrons may be bent backward, presumably to clear the pelvic outlet”. This higher backward slope of the first haemapophyses can be observed in *Brachylophosaurus canadensis* (see Prieto-Márquez 2001: fig. 52); *Gryposaurus notabilis* (see Parks 1920: pl. 1); *Saurolophus osborni* (see Brown 1913a: pl. 63) and *S. angustrostris* (see Maryánska & Osmólska 1984: 126); *Edmontosaurus regalis* (see Lull & Wright 1942: pl. 12B); and possibly *E. annectens* (see Lull & Wright 1942: pls 13 and 15 [it is shown in mounted skeletons] and *Prosaurolophus maximus* (see Parks 1924: pl. 5 [also a mounted skeleton]). This is the condition in the holotype of *T. insularis* too (Figs. 1 and 4A-B). The posterior inclination of the proximal chevrons occurs also in *Iguanodon bernissartensis* (see Norman 1980: fig. 47). Only the first chevron has a different slope in *Xuwulong yueluni* (see You et al. 2011: fig. 2), *Mantellisaurus atherfieldensis* (see Norman 1986: fig. 39) and *Corythosaurus casuarius* (see Lull & Wright 1942: pl. 27A). In the indeterminate hadrosaurid TMP 1998.058.0001, only the first two chevrons are shorter and more inclined backward than the others (Fig. 7A). In *Tenontosaurus tilletti*, the first two chevrons are only much shorter than the others but are not more inclined backward and do not touch each other (Forster 1990: fig. 5). Non-avian theropods (e.g., Gilmore 1920: pls 16, 22, 29, 30 and 35; Russell 1972: figs 1, 4 and pl. 1; Holtz 2004: fig. 5.8; Holtz et al. 2004: fig.4.8; Carpenter et al. 2005: fig. 3.14; Paul 2010; Persons et al. 2015); basal sauropodomorphs (Galton & Upchurch 2004: fig. 12.1; Paul 2010); sauropods (Upchurch et al. 2004: fig. 13.1; Paul 2010; Otero et al. 2012: figs. 4B-C and 5B); basal thyreophoran (Norman et al. 2004: fig. 15.4; Paul 2010); stegosaurs (Paul 2010); ankylosaurs (Carpenter 1997: fig. 22.2; Paul 2010); basal iguanodontians (Norman 2004: fig. 19.13; Paul 2010); heterodontosaurids (Paul 2010); pachycephalosaurs (Paul 2010); basal neoceratopsians (Forster & Sereno 1997: fig. 23.4; Hailu & Dodson 2004: fig. 22.2; Paul 2010); and ceratopsids (Forster & Sereno 1997: fig. 23.5; Paul 2010) are not reconstructed with the first five haemapophyses that are more backward inclined than the following ones and contacting each other. Therefore, this arrangement of the first haemapophyses seems to occur only within derived iguanodontians.

Unlike sauropods (Wilhite 2003; Otero et al. 2012) and some non-avian theropods (Persons & Currie 2011a), there is little change of form throughout the chevron series in hadrosaurids (Lull & Wright 1942: 81). The boot-like and the following bilobate chevrons of the holotype of *T. insularis* are not reported in any other hadrosauroids, whose haemal arch spines are just laterally compressed, finger-like rods without any anterior or posterior processes (e.g., Lull & Wright 1942; Norman 1986, 2004; Horner et al. 2004).

A change in chevron shape along the tail similar to that observed in the holotype of *T. insularis* occurs in some sauropods (e.g., *Mamenchisaurus*, *Shunosaurus* and *Diplodocus*; Otero et al. 2012: fig. 4B-C) and in ornithomimid (Russell 1972: figs. 1 and 4; Persons & Currie 2011a: figs. 5-6) and tyrannosaurid theropods (Lambe 1917: figs. 5, 14 and 19; Matthew & Brown 1923: figs. 2 and 4; and Brochu 2003: fig. 68). A specimen of the tyrannosaurid *Gorgosaurus* has chevrons very similar to the boot-like chevrons 12-13 of the holotype of *T. insularis* (with an extremely long posterior process of the spine; Persons & Currie 2011a: fig. 7). The extant crocodilians *Caiman* and *Paleosuchus* also show a similar pattern (Frey 1982: fig. 36). The dromaeosaurid theropod *Deinonychus antirrhopus* has bilobate 'proximal' chevrons that resemble the distal chevrons of *T. insularis* (Ostrom 1969: fig. 40A). Therefore, the shape of the haemal arches of *T. insularis* is unusual within the hadrosauroids but not within the Dinosauria.

In theropod and sauropod dinosaurs, the morphology of the spine of the boot-like and bilobate haemal arches is supposed to reflect the relationships between the CFL and the *M. ilioischiocaudalis* (*M. iliocaudalis* + *M. ischiocaudalis*) and to be indicative of size and extent of the CFL (Wilhite 2003; Persons & Currie 2011a; Otero et al. 2012). In these dinosaurs, the change in the shape of the haemal spine from digit-like to asymmetrical (i.e., boot-like) is supposed to be related to the tapering of the CFL, which is observed in extant crocodilians (Persons & Currie 2011a). In dinosaurs, this tapering would be recorded by "diagonal scarring" (Persons & Currie 2011a: 119) on the lateral surface of the haemal spine ("blade") of a few asymmetrical (i.e., boot-like) and forked (i.e., bilobate) chevrons (Persons & Currie 2011a: figs. 5-7; Otero et al. 2012: fig. 5B). This "scarring" is identified as the trace of the septum that divided the CFL from the *M. ilioischiocaudalis* (Wilhite 2003; Persons & Currie 2011a; Otero et al. 2012) and occurs in haemal arches located just anterior the disappearance of the pleurapophyses in theropods (Persons & Currie 2011a: 119), whereas it is found in the haemapophyses set in correspondence of the reduction "in size and development" of the pleurapophyses in the sauropod *Diplodocus* (Otero et al. 2012: 251). According to Persons & Currie (2011a: 125), "the anteroposterior ascent and eventual posterior disappearance of this scar is, therefore, taken to mark the *M. ilioischiocaudalis*' gradual dorsal intrusion and eventual usurpation of the *M. caudofemoralis*".

As seen above in the description of *T. insularis*, a "diagonal scarring" like that reported by Persons & Currie (2011a) and Otero et al. (2012) cannot be clearly identified in the haemal arches of the holotype of *T. insularis*. The spines of haemal arches 12 and 13 show faint and posteroventrally to anterodorsally oriented ridges (Fig. 6E-F); distinct fine striations with a similar direction are spread over the spine of haemal arch 13 (Fig. 6F). Diagonal fine striations occur also in the distal part of the spine of the other boot-like haemal arches (Fig. 6B-D). However, the orientation of these striations is opposite to that of the "diagonal scarring" reported by Persons & Currie (2011a) and Otero et al. (2012). Therefore, a relationship between the shape of the haemal arch and the relative position of the CFL and *M. ilioischiocaudalis* is not clearly established in *T. insularis*. Furthermore, there is no correspondence between the disappearance of the pleurapophyses, change in shape of the haemal arches and their reduction in size in *T. insularis*. In the holotype, the haemal arches gradually decrease in size from haemal arch 6 to 14 (caudals 12/13 to 20/21), pleurapophyses disappear at caudal 13 or 14 and the boot-like haemal arches 12-13 articulate on caudals 18-19 and 19-20, thus they are posterior to the last pleurapophyses.

Ibiricu et al. (2014: 469) hypothesized that "ventrally broad haemal arches [of the proximal caudals] may correspond to an increased surface of attachment for the CFL" in large titanosaurian sauropods.

As in crocodilians, the broad haemal spines with anterior and posterior processes gave more room also for the insertion of the interhaemal ligaments (Frey 1988: fig. 17; Schwarz-Wings et al. 2009).

The distally expanded haemal spines could have provided more surface for the attachment of the *M. ischiocaudalis* (see Arbour 2009: fig. 9; Persons

& Currie 2011a: fig. 2B), not only in correspondence of the tapering of the CFL, but also posterior to its disappearance.

Tail stiffness. The caudal vertebrae of *T. insularis* show two features that have often been considered to increase the tail rigidity: nearly vertical articular facets of the zygapophyses and presence of epaxial ossified tendons (e.g., Forster 1990; Maxwell & Ostrom 1995).

The nearly vertical articular facets of the zygapophyses limit long axis rotation and lateral flexibility of the tail, although flexibility increases posteriorly as zygapophyses reduce in size (Schwarz-Wings et al. 2009). However, steeply inclined articular facets of the zygapophyses alone do not totally hinder the lateral flexibility of the tail, as it is demonstrated by the curled tails of living and fossil archosaurs with steeply inclined articular facets of the zygapophyses (Frey 1982; Maxwell & Ostrom 1995: fig. 2; Ford & Martin 2010: 334).

The ossified epaxial tendons are an ornithischian synapomorphy (Sereno 1986). In the basal iguanodontian *Tenontosaurus tilletti*, ossified tendons "extend to the end of the tail" (Forster 1990: 280) and occur also hypaxially. They end at about caudal 20 in *Iguanodon bernissartensis* (see Norman 1980) and *Mantellisaurus atherfieldensis* (see Norman 1986). According to Horner et al. (2004: 453), ossified tendons extend "caudally to about the midsection of the tail". In the saurolophine hadrosaurid *Brachylophosaurus canadensis*, the lattice of ossified tendons is developed up to caudal 15, then ossified tendons are arranged parallel to the curvature of the tail (Prieto-Márquez 2001: 154). Ossified tendons seem to reach at about caudal 25 in the lambeosaurine *Corythosaurus casuarius* (Brown 1916: pls. 13-14). Their function in *T. insularis* is plausibly the same as in the other iguanodontians, not a specialization. The ossified tendons trellis of the hadrosaurids restricted the dorsoventral tail oscillation increasing spinal rigidity in the dorsoventral plane (Horner et al. 2004; Persons & Currie 2012) and reinforced proximally the tail against dorsoventral shear (Schwarz-Wings et al. 2009). However, they did not prevent the lateral motion of the tail (Organ 2006). An important feature of ossified tendons is to store and release elastic energy in a more effective way than non-mineralised tendons (Organ 2006), thus these structures helped in the quick recover after lateral bending of the tail.

Nearly vertical articular facets of the zygapophyses and presence of epaxial ossified tendons occur also in other hadrosauroids and did not make the tail of *T. insularis* peculiarly rigid. However, *T. insularis* presents other features suggesting a comparatively higher stiffness of the proximal portion the tail. The passive rigidity of this portion of the vertebral column was increased by the unusually broad pleurapophyses and neural spines (Hildebrand & Goslow 1998). The anteroposteriorly expanded neural spines favoured the apical insertion of the supraspinous ligaments, which stiffen the tail dorsally, and reduced interspinal lengths; likewise, the anteroposteriorly broad haemal spines stiffened the tail ventrally (Schwarz-Wings et al. 2009). The elongation of the centra reduced the density of intervertebral flexure points lowering the degree of tail flexibility per unit of absolute tail length (Persons et al. 2014).

Thus, the deeper proximal part of the tail of *T. insularis* was relatively rigid and quick in recovering from lateral oscillations, whereas the low distal part, with small zygapophyseal surfaces and without ossified tendons, was probably freer to move on the vertical and lateral planes. The low and more mobile distal part of the tail might have been used as a whip, possibly for courtship, intraspecific signalling and sexual display (Myhrvold & Currie 1997).

Tail musculature. As in crocodilians and in the muscular reconstructions of other non-avian dinosaurs, the principal epaxial muscles of the tail of *T. insularis* were the *M. transversospinalis* system and the LCA, the latter extending along the whole tail. The first inserted onto the lateral side of the neural spine, the other onto the lateral side of the neural pedicels (the base of the neural arch) and the dorsal side of the pleurapophyses in the proximal caudals and on the dorsal side of the centrum in the middle and distal caudals (Frey 1988; Arbour 2009; Persons & Currie 2011a; Mallison 2011). Therefore, these muscles had broad insertion surfaces in *T. insularis*. Actually, the *M. semispinalis* and *M. spinalis* of the *M. transversospinalis* system were anchored to the bone by tendons that originated and attached to the margin of the spine (Organ 2006), thus it is the shape of the spine more than its anteroposterior surface to favour their insertion. Up to caudal 20 of SC 57021, tendons of *M. semispinalis* were ossified, revealing the presence of this muscle.

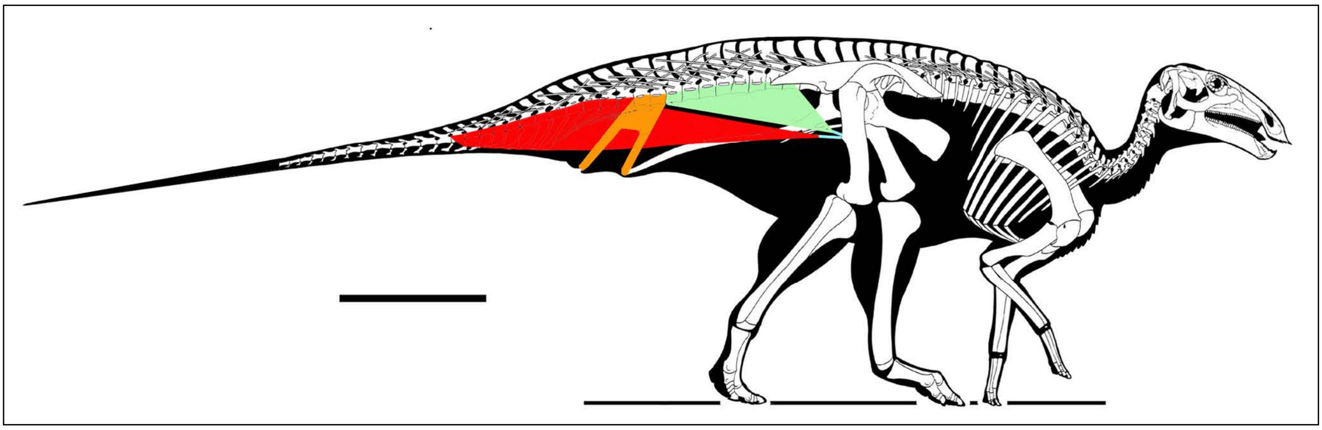

Fig. 17 - Reconstruction of the *M.m caudofemorales* and *M. transversus perinei* in *Tethyshadros insularis*. Reconstruction is based on the relationships of *M.m caudofemorales* and skeletal elements in extant crocodilians and limbed squamates. Red, *M. caudofemoralis longus*; green, *M. caudofemoralis brevis*; orange, *M. transversus perinei*. Skeletal reconstruction is by M. Auditore, muscle reconstruction is by the author. The scale bar equals 500 mm.

The anteroposterior breadth of the neural spines and pleurapophyses are much less important than their proximodistal elongation in assessing the development of the epaxial musculature (Persons & Currie 2011a,b, 2014). As the caudal neural spines of *T. insularis* are comparatively lower than those of lambeosaurine hadrosaurids and the pleurapophyses are not particularly long proximodistally, the proximal caudal epaxial musculature of *T. insularis* was comparatively less developed (see Persons & Currie 2014) than in lambeosaurine hadrosaurids, which were the most common hadrosauroids in the latest Cretaceous European Archipelago. However, the peculiar broadness of the neural spines and pleurapophyses of SC 57021 imply that intrinsic *Mm. interspinales* and *Mm. intertransversarii* were shorter than in other hadrosauroids.

Posterior to the disappearance of the pleurapophyses, the ventral limit of the LCA was probably marked by the sharp longitudinal ridge located in the dorsal part of the lateral surface of the centrum (caudals 15-22; SI, Fig. 1), whereas this muscle had probably a broad ventral insertion on the flat dorsal side of the hemicylindrical centra of caudals 23-33 (cf. Frey 1988: fig. 46C; SI, Fig. 2C and D). Plausibly, the *M. transversospinalis* system sensibly reduced its size or disappeared with the neural spine reduction around caudal 20 (cf. Frey 1988: fig. 46; Schwarz-Wings et al. 2009: fig. 9E).

The main hypaxial muscles in the tail were the *Mm. caudofemorales* (CFL [see above] and *M. caudofemoralis brevis*, CFB), *M. ischiocaudalis* and *M. iliocaudalis*.

In extant crocodilians, the CFL inserts via tendon onto the 4th trochanter of the femur, whereas the CFB inserts onto a slightly more proximal position (Frey et al. 1989; Otero et al. 2010).

In extant crocodilians, the origin of the CFL is strictly related to the haemal arches (Frey 1982; Wilhite 2003; Persons & Currie 2011a; Otero et al. 2012; Ibiricu et al. 2014). The point of origin of the CFL that is closer to its femoral insertion is onto the first haemal arch, whereas the insertion onto the ventrolateral surfaces of the centra starts more posteriorly (Frey 1982). The strict relationship of the CFL with the first chevrons is observed also in limbed squamates (e.g. Russell et al. 2001; Persons & Currie 2011a; Ibiricu et al. 2014). The CFL is the main femoral retractor in extant reptiles (Gatesy 1990; Otero et al. 2010; Persons & Currie 2011a; Ibiricu et al. 2014) and is considered to have had a pivotal importance in the locomotive power stroke of non-avian dinosaurs (Romer 1927; Gatesy 1990; 1995; Persons & Currie 2011a, 2014).

In the extant crocodilian *Caiman latirostris*, the CFB originates on the posteroventral portion of the ilium and on the lateral sides of the centrum and ventral side of the pleurapophyses of the first caudal vertebra (Otero et al. 2010: 176), which is the only caudal vertebra not to bear a chevron in crocodilians, as the first chevron usually articulates between caudals 2/3 (Erickson et al. 2005). This location of the CFB origin has been reported also from other crocodilians (Ibiricu et al. 2014: 456, 462 and tab. I). In non-avian theropods and sauropods, the CFB has consequently been reconstructed as originating from the proximal, chevron-less caudal vertebrae (Persons

& Currie 2011a: fig. 9; Ibiricu et al. 2014: fig. 6). The CFB is a femoral retractor as the CFL but it is considered to have had a secondary role in the locomotive power stroke of non-avian dinosaurs (Romer 1927; Gatesy 1990; Persons & Currie 2011a).

Inferring this origin for the *Mm. caudofemorales* in *T. insularis*, the chevron-less vertebrae 1 to 6 or 7 and their broad pleurapophyses were the place of origin of the CFB, whereas the origin of CFL was displaced posteriorly in the tail (Fig. 17). Because the first chevron has shifted to a more distal position and consequently the first chevrons are shorter than they would be if they were located more proximally, the proximal transversal section of the CFL, where the muscle is deeper, is lesser in *T. insularis* than in other hadrosauroids with a more proximally placed first chevron.

The "transition point" (sensu Gauthier 1986:19) and the distal-most extent of the CFL origin (Gatesy 1995) can be located around caudal vertebra 20 (rather posterior to the last pleurapophyses) in the holotype of *T. insularis*.

Maintaining the proportions, the shape and the relationships with the skeletal elements that the reconstruction of the CFL has in other dinosaurs (Wilhite 2003: fig. 5.13; Gallina & Otero 2009: fig. 7; Persons & Currie 2011a: figs. 9 and 11, 2011b: fig. 3, 2012: fig. 5, 2014: fig. 26.2; Persons et al. 2014: figs. 7-9; Otero et al. 2012: fig. 5; Ibiricu et al. 2014: fig. 6), this muscle results to be comparatively shorter and much more slender in *T. insularis* than in other dinosaurs and its place of origin extends along the vertebral column less than half the length of the whole muscle and its tendon (Fig. 17). Conversely, the CFB results be comparatively much more developed and its role in femur retraction would be more relevant than in other reptiles.

It might be possible that, unlike extant reptiles but like the *M. caudofemoralis pars caudalis* of the ostrich (Ibiricu et al. 2014), the CFL of *T. insularis* originated also from the lateroventral sides of the centra of the chevron-less caudals, and possibly also from the ventral side of their pleurapophyses. In that case, the CFB might be relegated to caudals 1-2 and/or the posteroventral side of the long postacetabular process of ilium; the CFL would be larger than in the reconstruction of figure 16 (which is based on its origin from the chevron-bearing vertebrae only), although its maximum cross-section would not be as deep as the muscle had originated from longer chevrons articulated to the first caudals. However, the development of *M. caudofemoralis pars caudalis* and *M. caudofemoralis pars pelvica* (which are the avian homologue of crocodilian CFL and CFB, respectively) is a consequence of the extremely short caudal segment of the vertebral column of the Pygostylia and the function of control over the tail feathers and is related to the ability to fly (Gatesy 1995; Ibiricu et al. 2014), which is obviously not the case of *T. insularis*.

In the crocodilian *Alligator sinensis*, the dorsal venter of *M. transversus perinei* (TP) originates from the surface of the centra of caudals 1- 4 and is connected by an aponeurosis to a ventral venter that is split into two parts, one inserting onto the distal end of the ischium and the other into the cloacal cartilage (Cong et al. 1998). According to Frey (1982), the origin of the dorsal venter of TP is on vertebrae 1-2 (i.e., the chevron-less vertebrae) in *Caiman* and *Paleosuchus*. TP wraps the CFL in extant crocodylians. If TP was present in *T. insularis*, it had to be much displaced posteriorly, as origin and insertion as well, with respect the other dinosaurs (Fig. 17).

Locomotion. The epaxial *M. transversospinalis* system and LCA and the hypaxial *M. ischiocaudalis* and *M. iliocaudalis* would function to bend the tail (Ostrom 1969; Arbour 2009). Synchronous contractions of the epaxial musculature produced tail extension in the vertical plane, whereas synchronous contractions of the hypaxial musculature resulted in ventral flexion (Schwarz-Wings et al. 2009). However, synchronous contractions of the epaxial and hypaxial musculature of both sides could stiffen the tail, avoiding oscillations and stabilizing it during locomotion. This may have helped *T. insularis* in maintaining balance during the irregular movements (cf. Ostrom 1969) involved in locomotion on a rough ground as that of a karst landscape.

As seen above, the CFL is considered to be the major contributor to the power stroke of the hind limbs in all gaits in non-avian dinosaurs (Gatesy 1990, 1995; Persons & Currie 2011a, 2014). Considering the reconstruction of the *Mm. caudofemorales* of *T. insularis* inferred from the relationship of these muscles with the skeletal elements in extant crocodilians (Fig. 17), the CFL of *T. insularis* has a comparatively shorter origin area, a much longer segment from the insertion on the femur to the closer origin on the first chevrons and a lesser maximum cross-sectional area than other dinosaurs with the tail musculature reconstructed in the same way, whereas it has a much larger CFB (Persons & Currie 2011a: fig. 9, 2014: fig. 26.2B and E; Persons et al. 2014: 7B1; Otero et al. 2012: fig. 5; Ibiricu et al. 2014: fig. 6). This has probably an impact in the role of those two muscles in locomotion and casts doubts about the analogy of their functions in crocodilians and *T. insularis*.

The cross-sectional area of the CFL at its greatest width is the most important parameter linked to the locomotive contribution of the muscle (Persons & Currie 2014). A comparatively lesser maximum cross-sectional area of the CFL than other dinosaurs would suggest a comparatively lesser contractile force (F_t) and torque exerted by this muscle in *T. insularis* with respect to the same muscle in a hadrosauroid with a more proximally placed first chevron (moment arm length being the same for the torque) (Persons & Currie 2011a, 2014). Furthermore, the torque of the CFL would be proportionally lower in *T. insularis* than in an average hadrosauroid, because the femur of *T. insularis* is much shorter than tibia (Fig. 17), whereas femur is usually slightly longer than tibia in hadrosauroids (Lull & Wright 1942; Norman 2004). In *T. insularis*, the point of insertion of the tendon of the CFL (and that of CFB as well) was proportionally closer to the joint's centre of rotation (acetabulum) than in those hadrosauroids. Therefore, the moment arm length (R, measured from the joint's centre of rotation and the muscle's insertion) was comparatively shorter in *T. insularis* than that of a hadrosauroid with a hind limb of the same length but with a proportionally longer femur, assuming that the 4th trochanter, which is not preserved in any *T. insularis* specimens, was in the same position in *T. insularis* as it is in the other hadrosauroids. According to lever mechanics, muscles inserting closer to a joint work at higher velocities; CFL insertion is more proximally located to the joint's centre of rotation in taxa that move more quickly (Persons & Currie 2011a, 2014; Maidment et al. 2012). Because of the posterior displacement of the origin of the CFL, the angle between the vector line of pull (equivalent to the orientation of the CFL tendon) and the vector orthogonal to the moment arm (θ) would be close to 0 (Fig. 17). As the effective force (F_e) that the muscle exerts is calculated with the equation $F_e = F_t \cdot \cos\theta$ (Persons & Currie 2011a: 122), the F_e exerted by the CFL of *T. insularis* was close to the F_t and the effectiveness of the joint was close to the maximum (Ibiricu et al. 2014: 15). This somewhat compensated the proportionally shorter moment arm length, as the potential torque generation (τ_m) is calculated with the equation $\tau_m = R\, F_e \cdot \sin\Phi$ (Φ is the angle between the vectors of the moment arm and the effective force, which is assumed to be 90° when the femur is positioned perpendicular to the ground; Persons & Currie 2011a: 122).

The shortening of the moment arm length, the posterior displacement of the CFL origin, with consequent elongation of the muscle but lowering of its maximum cross-sectional area, and the comparatively larger CFB suggest that the locomotor abilities of *T. insularis* were somewhat different from those of the other hadrosauroids (Persons & Currie 2011a, 2014). This may be an adaptation to its peculiar life environment: locomotion on the uneven and rugged karst ground instead of that flat and regular of the flooding and coastal plains. It may be a modification to climb, jump or walk on rugged stony grounds rather than to reach a more or less fast or sustained locomotion. As an alternative, the tail musculature of *T. insularis* might just be reshaped as a consequence to the posterior shift of the vent, which would be the main adaptation of this dinosaur, in order to obtain the same locomotor performance as other hadrosauroids.

However, also limb features support an adaptation of *T. insularis* to a peculiar style of locomotion. The manus of *T. insularis* is similar to that of the hadrosaurids in its overall structure (Brown 1912; Lambe 1913; Parks 1920: fig. 13). Humerus, radius and ulna and their articulation (Dalla Vecchia 2009c: figs 1 and 6) is like that of other hadrosauroids (Norman 1986, 2004; Horner et al. 2004; Brett-Surman & Wagner 2007), with the radius parallel to ulna and firmly set in front of it and the manus with the palm facing mediocaudally (Senter 2012). Manus/forelimb length ratio (metacarpal III length/radius+humerus length ratio) is 0.226 and 0.210 (because of the different length of the right and left bones; Dalla Vecchia 2009c: tab.1) in the upper range of the Hadrosauridae, whose elongation of the manus is possibly an autapomorphic feature (Maidment & Barrett 2014: 58). Radius/humerus ratio (0.922 and 0.975) is within the range of basal and saurolophine hadrosaurids (Lull & Wright 1942: tabs 4-8; Maidment & Barrett 2014: 60).

Forelimb/hind limb length ratio (radius+humerus length/femur + tibia length ratio, 0.584) is that usual for hadrosauroids (Maidment & Barrett 2014: tab. 2). However, the hands of *T. insularis* are tridactyl because they lost digits V, which were not involved in support during locomotion, anyway (Dilkes 2000: fig. 3). The remaining digits II-IV of *T. insularis* had no grasping abilities, because the distal articular surfaces of the metacarpals are flat (Fig. 16B) and phalanges II-2 and III-2 are short and wedge-shaped (Fig. 16A-B) (see also Maidment et al. 2012: 6-7). Extension and flexion were not possible at the metatarsal-phalangeal joints and at the phalangeal joints, with the possible exception of the phalangeal joint of the phalanx III-1. However, phalanx III-1 seems to be fused with the metacarpal III in the right manus of SC 57022 (Fig. 16D). Furthermore, the elongated metacarpals are tightly appressed to form a single functional unit, the phalangeal portion of the manus is very short (Fig. 16) and the carpus is reduced to a single, very small and rounded carpal (Fig. 16A). Ungual phalanges of digits II and III are hoof-like, but digit IV lacks a hoof-like ungual phalanx (Fig. 16B-D). The manus of *T. insularis* has on the whole the aspect of a pillar.

Unlike all other hadrosauroids, the tibia is much longer than femur in *T. insularis* (femur/tibia length ratios is 0.76; Dalla Vecchia 2009c). The pes/hind limb length ratio (metatarsal III/femur+tibia length ratio, 0.199; see Dalla Vecchia 2009c: tab.1) is slightly higher than in hadrosaurids (Lull & Wright 1942: tabs 4-7; Maidment & Barrett 2014: 63), but this ratio is negatively size-correlated in ornithischians (Maidment & Barrett 2014: 65). The pedes have very short phalangeal portions (SI, Fig. 6A), even shorter than those already short of the hadrosaurids (e.g., *Maiasaura peeblesorum*, see Dilkes 2000: fig.12G-H; *Saurolophus* sp., Moreno et al. 2006: fig. 3E; SI, Fig. 6B). Non-ungual phalanges distal to those of the first ray are disc-like and ungual phalanges are hoof-like and much wider than long. Digit mobility was possible only at the metatarso-phalangeal joint and between phalanges 1 and 2.

Modifications from the basal hadrosauroid pattern occurred in *T. insularis*' manus and pes reduced the mass of the limbs (Hildebrand & Goslow 1998) and are a further development toward the subunguligrade posture shown by the hadrosaurids (Moreno et al. 2006). *T. insularis* shows a puzzling mixture of features suggesting both quadrupedality (subunguligrade posture, hoof-like manual ungual phalanges and broad supracetabular process of ilium) and bipedality (femur much shorter than tibia and comparatively high pes/hind limb length ratio) (Maidment & Barrett 2014).

Reduction of the mass of the limbs, vertebral column rigidity reducing oscillating motions, short and robust femur, long and slender tibia, long and compact metatarsus, CFL attachment located proximal along the leg, high radius/humerus ratio (slender radius-ulna) and digitigrade manus with long and tightly appressed metacarpals are 'cursorial' features (Coombs 1978; Hildebrand & Goslow 1998; Maidment et al. 2012). However, according to Maidment et al. (2012: 3) "cursorial morphology has not always been found to closely correlate with maximum running speed in extant mammals, and it may correspond with other features of locomotor performance, such as stamina or locomotor efficiency at slow speeds".

According to Brown (1912: 107), the manus of the hadrosaurid *Edmontosaurus* "was no longer used to any extent in progression" because of "the extreme elongation of the metacarpals, the loose articulation of the phalanges and the reduction of the unguals to two functional hoofs". Gracility of the mani of the holotype of *T. insularis* and their small bearing surfaces (Fig. 16A) suggest that they might not be used primarily for weight-bearing (a hypothesis already advanced by Ostrom 1964: 994 for hadrosaurs based on the reduced carpus). Mani might be employed for steering and to balance the vertical and lateral oscillations of the anterior part of the body during locomotion, which would be particularly useful on an uneven rugged ground.

Position of the first haemal arch and concomitant elongation of the ischium. In reptiles, haemal arches usually begin at about the third to seventh caudal (Romer 1956: 267). According to Horner et al. (2004: 453) the first haemal arch is distal to caudal 2 or 3 in lambeosaurines and distal to the fourth or fifth caudal in the other hadrosaurids. The first haemal arch occurs between caudals 4 and 5 in the saurolophine *Edmontosaurus annectens* (see Lull & Wright 1942: 79), *Gryposaurus notabilis* (see Parks 1920: pl. 1) and *Saurolophus osborni* (see Brown 1913a: 389) and in the lambeosaurine *Nipponosaurus sachalinensis* (see Suzuki et al. 2004: 152); it is located between caudals 3 and 4 in the indeterminate hadrosaurid TMP

1998.058.0001 (not considering the caudosacral in the count of the caudals; see above). The first haemal arch occurs between caudal 2 and 3 in *Iguanodon bernissartensis* (see Norman 1980: fig. 47), *Mantellisaurus atherfieldensis* (see Norman 1980: 308, fig. 39) and the non-hadrosaurid hadrosauroid *Xuwulong yueluni* (see You et al. 2011: fig. 2); it occurs between caudal 1 and 2 in the basal iguanodontians *Tenontosaurus tilletti* (see Forster 1990: fig. 5), *Dryosaurus altus* and *Dysalotosaurus lettowvorbecki* (see Galton 1981: 280).

Therefore, the position of the first haemal arch appears to be somewhat biased phylogenetically and it is more distal in the tail in saurolophine hadrosaurids than in most other iguanodontians. However, *T. insularis* has apomorphically an even more distal position of the first chevron and a consequent elongation of the ischiadic shaft, unlike all other iguanodontians and dinosaurs in general.

The absence of the haemapophyses in the most proximal caudals is related to the presence of the cloaca and associated structures (Williston & Gregory 1925: 110; Romer 1956: 267). The posteriorly displaced first haemal arch and the concomitant elongation of the centra displace posteriorly the vent and copulatory organs, lengthening the terminal tract of the intestine (colon) and possibly the cloaca too. This is the main morphological peculiarity of *T. insularis'* tail and has important consequences also on the tail musculature. As this feature occurs in both specimens SC 57021 and SC 57247, it is unrelated to their different body robustness and is plausibly linked to a function that was advantageous in the environment where these dinosaurs lived.

The three main sources of body water loss in reptiles are respiration, nitrogenous excretion and transpiration through the body surface (Minnich 1982). In reptiles, the cloaca and colon modify the urine produced by the kidneys and regulate renal water (Minnich 1982). In crocodilians, which lack a bladder, the cloaca and colon are the main urinary storage sites (Minnich 1982). The reptilian cloaca usually absorbs water, sodium and chlorine and secretes urates (Minnich 1982); the urodaeum of the cloaca is the primary site for urine modification in crocodilians and is capable of storing large quantities of urine (Kuchel & Franklin 2000). In birds, the colon is not only important for water absorption from food, but also for its reabsorption (together with caeca) from ureteral urine (post-renal water) (McLelland 1990; Duke et al. 1995; Musara et al. 2002), although this is variable in different birds. In the ostrich (*Struthio camelus*), there is no post-renal water reabsorption (Skahdauge et al. 1984; Duke et al. 1995) and the large size of the colon is an important anatomical adaptation to maximise the absorption of the ingested water (Musara et al. 2002). In birds where the colon is relatively short "colonic water absorption is maximised by retrograde flow of urine into the lower gastrointestinal tract"; Musara et al. 2002: 318). Possibly, the longer colon of *T. insularis* would maximise water absorption or a longer colon and/or cloaca would store more urine and allow maximising post-renal water reabsorption in case of dehydration. The elongation of the colon and possibly cloaca suggested by the posterior shift of the vent could be an adaptation to a fresh water depleted environment, as is the case of an emergent carbonate platform with its prevailing underground water flow, and subject to drought events affecting also the development of the vegetation (possibly the main source of water for this vegetarian dinosaur).

The posterior shift of the vent and the consequent distal genital position (McLelland 1990; Ziegler & Olbort 2007) might have also reproductive implications. For example, it might make breeding easier, although no clear advantage seems to derive from the posterior shift of the vent, if hadrosauroids copulated as reconstructed by Isles (2009). This aspect cannot be further investigated, because we do not have much information about hadrosauroid genitals and copulation (Isles 2009).

The posterior shift of the vent implies also the elongation of the oviducts in females, if the shift does not correspond to a proportional elongation of the cloaca posterior to the opening of the oviducts into the urodeum. Extant crocodilians have two functional oviducts, ovulated all the eggs at the same time and "eggshells are calcified in assembly-line fashion along the oviduct, followed by simultaneous oviposition" (Schweitzer et al. 2007: 1156, see also fig. 1; see Fox 1977, and Zelenitsky & Hills 1997). Extant birds have a single functional oviduct and produce one egg at a time (Varricchio et al. 1997; Zelenitsky & Hills 1997). At least some non-avian theropods had two functional oviducts and produce one egg per oviduct at a time (Varricchio et al. 1997; Sato et al. 2005; Zelenitsky 2006; Yang et al. 2019). Hadrosaurids are supposed to have had two functional oviducts and to produce more than one egg per oviduct at a time like crocodilians (Zelenitsky & Hills 1997; Yang et al. 2019). Under these assumptions, longer oviducts meant more room for a comparatively higher number of fertilized eggs; *T. insularis* would produce clutches composed of a comparatively higher number of eggs respect to other hadrosauroids with a proportionally shorter oviduct, the egg size remaining comparable. This might be an adaptation of an insular r-strategist taxon (see Raia et al. 2003) to the variable and harsh environmental conditions (mainly about water supply) of the Adriatic island.

CONCLUSIONS

The minimum estimated total length of the distally incomplete tail of the holotype of *T. insularis*, based on the proportional centrum-by-centrum scaling respect to the complete tail of a hadrosaurid from the Upper Campanian of Canada, is over 2.5 metres and accounts for 56% of the total body length. The tail of *T. insularis* was rather long and its portion posterior to vertebra 20 was probably whip-like.

The two main specimens of *T. insularis* differ in robustness, in the shape of the haemapophyses and possibly in the shape of the pleurapophyses. These differences may represent sexual dimorphism (as it has been suggested for other dinosaurs), although ontogeny or high intraspecific variability due to the insular condition might be alternative explanations.

Comparison between the caudal vertebrae of *T. insularis* and those of the latest Cretaceous hadrosauroids that lived in the European archipelago shows that the vertebrae of the Italian taxon differ from those of the other hadrosauroids, although the first caudals show some resemblance with those from Romania, which may belong to *Telmatosaurus transsylvanicus* (a taxon that is found to be close to *T. insularis* in some phylogenetic analyses). The peculiar features of the caudals of *T. insularis* (vertebral centra longer than high also in the proximal elements; centra of the posterior mid-caudals with the shape of amphicoelous semicylinders; pleurapophyses of the first five caudals broad and tongue- or fan-shaped; apically broad neural spines in lateral view, which gradually change in shape from meat cleaver-like in the first proximal caudals, to fan- or spatula-shaped in the posterior proximal and first mid-caudals, to ‘petaloid’ in the following mid-caudals; haemal arches changing in shape along the tail from rod-like to boot-like to bilobate; and first haemal arch set between caudals 7-8 or 8-9, with a long, chevron-less proximal segment of the tail) are not found in the other insular hadrosauroids of the European archipelago as well as in continental hadrosauroids and are confirmed as apomorphic traits of the Italian taxon.

These apomorphies cannot be a only a consequence of insularity, because all of the hadrosauroids from the European archipelago were insular dwellers but they are more conservative than *T. insularis*. The tail apomorphies of *T. insularis* may be related to the karst landscape where the Italian dinosaur lived. Skeletal features suggest that the long tail was relatively stiff and deep proximally, whereas it was whip-like and more movable distally. The reconstruction of the tail musculature based on comparison with that of living archosaurs and the reconstructed musculature in other non-avian dinosaurs, shows that the posterior shift of the first chevron affected the size and shape of the *M. caudofemoralis longus*, which is usually the major contributor to the power stroke of the hind limbs in reptiles, and of the *M. caudofemoralis brevis*. This different development of the hypaxial musculature would probably have important consequences on the locomotion of *T. insularis*, and may be related to its life habits too. The posterior displacement of the origin of the *M. caudofemoralis longus*, with consequent elongation of the muscle but lowering of its maximum cross-sectional area, the shortening of its moment arm length, and the comparatively more developed *M. caudofemoralis brevis*, suggest that the locomotor abilities of *T. insularis* were somewhat unlike those of the other hadrosauroids. This is indicated also by some peculiar limb features (including a compact tridactyl manus without grasping ability and with a small bearing surface, short phalangeal portions of the pedes and tibia much longer than femur) suggestive of quadrupedality as well bipedality and a cursorial locomotor mode. These may be adaptations to an effective locomotion (by climbing, jumping or walking) on the stony and rugged karst ground rather than to reach a fast or sustained locomotion. Stiffening of the tail, increased by synchronous contractions of the epaxial and hypaxial musculature of both sides, would avoid its oscillations and stabilize it during locomotion on the rough ground. The forelimbs, with their pillar-like mani, may be used for steering and to balance the oscillations of the anterior part of the body.

The posterior shift of the vent suggested by the posterior position of the first haemapophysis implies a longer distal tract of the intestine or a longer cloaca, which could increase the space for water absorption or urine storage and urinary water reabsorption, an advantage in the water-depleted karst where the animal lived. In the case of a normally-sized cloaca, the posterior shift of the vent would imply also longer oviducts and plausibly an increased number of eggs per clutch, also a possible advantage in the stressing life environment of *T. insularis*.

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