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New hybondontoid shark from the Permocarboniferous (Gzhelian–Asselian) of Guardia Pisano (Sardinia, Italy)

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Numerous isolated teeth, fin spine fragments and dermal denticles of a hybodont shark from a lacustrine limestone horizon at the top of lithofacies B of the Late Carboniferous to Early Permian succession of the Guardia Pisano Basin (Sulcis area, southwestern Sardinia, Italy) are assigned to a new species of the genus *Lissodus* Brough, 1935. *Lissodus sardiniensis* sp. nov. is erected on the basis of about 500 teeth, which show a unique feature of only one pair of lateral cusps that are bent in the direction of the prominent central cusp. Weak heterodonty allows distinction of symphyseal, mesial to anterolateral, and lateral teeth. *Lissodus sardiniensis* sp. nov. was a freshwater-adapted durophagous shark of bottom dwelling habit, an interpretation supported by general construction of the dentition and the morphology of the dermal denticles. The association with *Acanthodes*, diplodoselachid sharks and branchiosaurs allows the reconstruction of a five-level trophic chain for the Guardia Pisano Basin. The discovery of *Lissodus* in Sardinia is presently the southernmost known occurrence of that genus in the Late Palaeozoic of Europe. This new find adds significantly to knowledge of migration routes of aquatic organisms, especially freshwater sharks, between the single European basins in the Late Pennsylvanian, and changes in palaeobiogeography during the Early Permian.

Key words: Chondrichthyes, Hybodontoidea, *Lissodus*, taxonomy, palaeoecology, palaeobiogeography, Sardinia, Italy.

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Introduction

Isolated remains of the chondrichthyan hybodontoid genus *Lissodus* are known so far from the European non-marine Late Carboniferous to Early Permian of Spain, France, Germany, Czech Republic, and Ukraine (Gebhardt 1988; Soler-Gijón 1993; Soler-Gijón 1997; Steyer et al. 2000; Zajíc 2000; Duffin 2001). The first record of *Lissodus* from the Guardia Pisano Basin (Sulcis) in SW Sardinia (Fig. 1) was reported by Freytet et al. (2002), and subsequently mentioned by Schneider et al. (2003) and Fischer et al. (2003). Intensified micropalaeontological processing of limestone boulders, sampled by J.S. during a field trip of the Brescia Symposium in 1999, has provided an extremely fossiliferous and diverse assemblage of isolated fish remains (Fischer 2005) as well as indeterminable branchiosaur-like jaw fragments (Werneburg et al. 2007). The fish assemblage is dominated by teeth, dermal denticles and fin spine fragments of a previously unknown species of *Lissodus*, and scales and fin spine fragments of *Acanthodes* sp.

The material described below is exceptional because of the large number (> 500) of isolated teeth and tooth fragments, > 150 dermal denticles and numerous fin spine fragments from only a small limestone sample of about 1 kg.

Institutional abbreviation.—FG, Geological Institute, Technical University Bergakademie Freiberg, Germany.

Other abbreviations.—LAD, last appearance datum; LOD, last occurrence datum; NM, find locality Niedermoschel, Germany; SCE, single crystallite enameloid.

Geological and stratigraphical setting

The Guardia Pisano Basin was a small intramontane trough located in the Sulcis area of SW Sardinia, Italy (Fig. 1), close to the village of Gonnesa (Barca et al. 1992; Pittau et al. 1999). Today, what remains of this basin is only an about 130 metre-thick continental volcano-sedimentary succession (Pittau et al. 2002; Barca and Costamagna 2006; Ronchi et al. 2008), which crops out on the road to Portoscuso. The depos-

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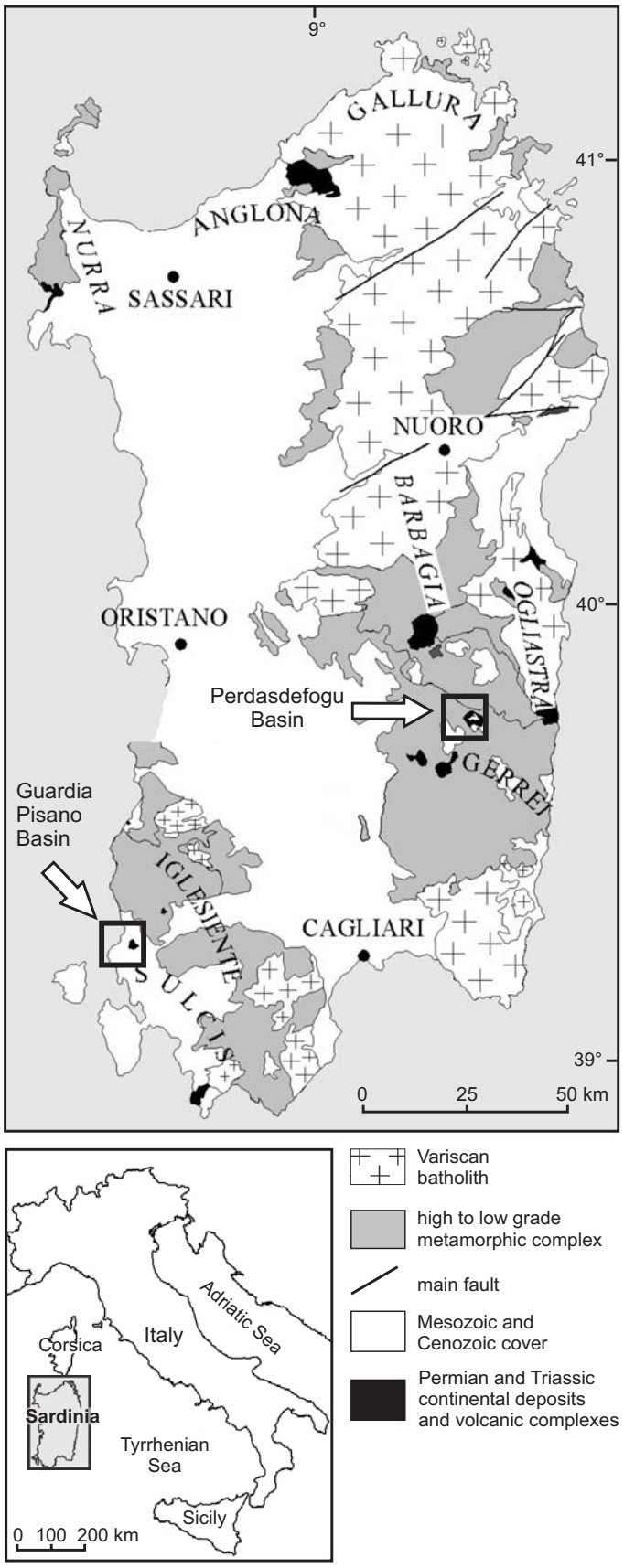

Fig. 1. Geological map of Sardinia with the locations of the Guardia Pisano and Perdasdefogu basins (modified from Werneburg et al. 2007).

its are generally divided into four informal lithostratigraphic units, separated by facies changes or unconformable stratigraphic contacts and covered by Eocene marine limestones (Fig. 2). The lower section comprises two units (Pittau et al. 1999): lithofacies A (Fig. 2), 6–7 m (base not exposed) of dark grey carbonaceous shales with sporadic sandstone lenses; and lithofacies B (Fig. 2), about 15 m of alternating carbon-rich shales, sandy dolostones, tuffs and brecciated rhyolitic and rhyodacitic lavas. Following an erosional unconformity, lithofacies C (Fig. 2) of the upper section follows with about 45 m of medium–fine-grained reddish sandstones and micaceous siltstones with interstratified conglomerate layers and dark shale lenses. This is unconformably overlain by lithofacies D (Fig. 2) with 60–70 m of purplish-red sandstones and pelites with repeatedly intercalated pebbly fine sandstones and conglomerates.

The depositional environment associated with volcanic activity shifts from blackish-grey sediments of a predominantly palustrine and fluvio-lacustrine system (lithofacies A, B) to grey and reddish sediments of a fluvial (C) to an alluvial plain system (D) under a hot and humid climate (Pittau et al. 1999, 2002; Barca and Costamagna 2006; Ronchi et al. 2008).

The lower unit yields a macroflora of pecopterid and conifer remains. Furthermore, lithofacies A has provided a microfloral assemblage (21 spore and 23 pollen genera, Pittau et al. 1999, 2002) in a very good state of preservation, indicating a meso- to xerophilic flora, which grew in a dry environment at tropical-subtropical latitudes. This palynological association allows a biostratigraphic comparison with the Gzhelian–Asselian of the Donetsk and Ural basins, the Early Wolfcampian (Asselian) of the North American Midcontinent and the Stephanian–Autunian (Gzhelian–Asselian) transition of Western Europe (Pittau et al. 1999). Radiometric determinations (SHRIMP and lead-zircon evaporation method) on the intercalated calcalkaline volcanic rocks of lithofacies B delivered a date of 297 ± 5 Ma (Pittau et al. 2002) that is in good agreement with palynological data. For the upper unit only an imprecise post-Asselian age can be assumed because of the absence of time-indicative fossils (Pittau et al. 2002; Ronchi et al. 2008).

The isolated vertebrate remains reported here were extracted from an 80–90 mm thick brownish-grey lacustrine micritic limestone, which covers a black pelite in the upper part of lithofacies B (Fig. 2) with an erosive junction. From the bottom to the top of the bed a transition from a peloidal micrite about 15 mm thick into a fine sandy siliciclastic micrite is observed with a concomitant increase in larger clasts from 2 to 10%. The peloids have a diameter of 0.2–2 mm, and associated cellular plant fragments (?wood particles) have a size range of 1–5 mm. The siliciclastic components are clay, silt and fine sand particles. The larger clasts consist of grey to beige, rounded limestone intraclasts of 1–5 mm diameter and 2–4 mm large charcoal particles. Pieces of twig-like petrified wood in the upper part of the limestone reach 20 mm in diameter. Aquatic invertebrates, ostracods and small (3 mm-long) gastropods, are rare. The C-org rich black pelite below the limestone contains isolated vertebrate remains in much higher

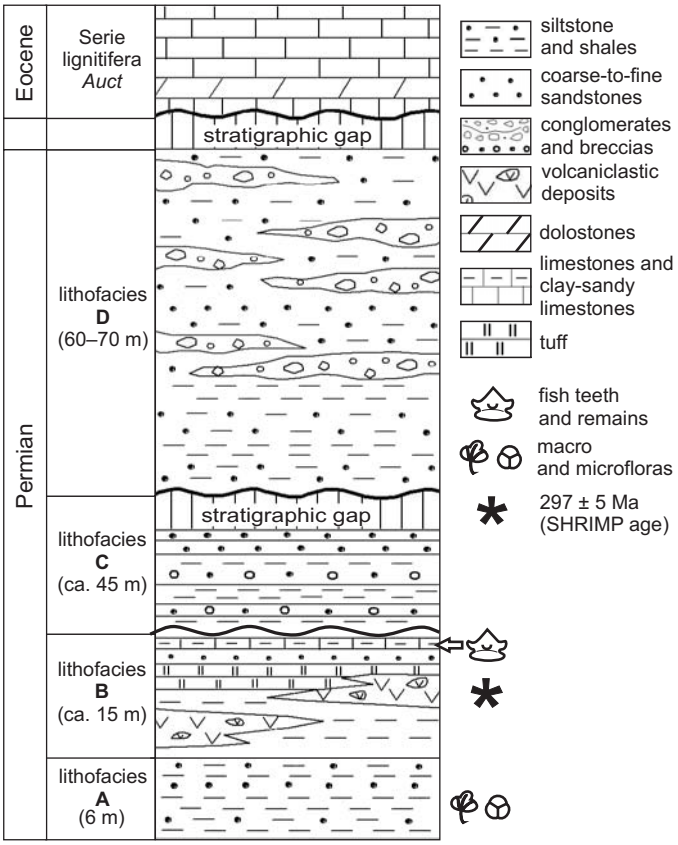

Fig. 2. Simplified stratigraphic section of the Guardia Pisano Basin (SW Sardinia) showing the position of the *Lissodus*-bearing horizon. Vertical distances are not time- or thickness-related (modified from Ronchi et al. 2008).

concentrations (~1%) than the limestone itself (< 0.5%). The unconformable contact between the limestone and the pelite, as well as the black colour of the vertebrate remains, indicate that the fossils were reworked from the black pelite. Intraclasts of this pelite were not observed. This may indicate that the pelite was still of muddy consistency during reworking. Because no trace of abrasion of the vertebrate remains is observable, significant transport can be excluded. Therefore, the occurrence of these remains is regarded as parautochthonous.

Methods

Two limestone samples of about 1 kg were processed with 10% formic acid. Microfossils were picked from the resultant residues under a binocular microscope and photographed with a Scanning Electron Microscope (JEOL JSM6400).

All material is housed at the Department of Palaeontology, Geological Institute, Technical University Bergakademie Freiberg, Germany. The specimens are catalogued as FG 589/… followed by T for tooth, F for fin spine fragment or S for scale, and a number. The descriptive terminology used (Fig. 3) is after Duffin (1985) for teeth, after Schneider (1986) for fin spines, and after Thies (1995) for dermal denticles.

Systematic palaeontology

The fossil record of *Lissodus* shows a widespread modern geographical distribution from Europe (Schneider et al. 2000; Steyer et al. 2000; Duffin 2001; Duncan 2004), Asia (Chang and Miao 2004; Prasad et al. 2004; Rees and Underwood 2006, Prasad et al. 2008), Australia (Trinajstic and George 2007; Susan Turner, personal communication 2008), North America (Zidek et al. 2004; Hunt et al. 2006; Milner and Kirkland 2006) and Africa (Brough 1935; Antunes et al. 1990; López-Arbarello 2004). The stratigraphic record comprises about 300 million years from the Late Devonian (Frasnian) to the Late Cretaceous (Maastrichtian) (Duffin 2001; Fischer 2008). Although *Lissodus* is found in rocks of marine origin in the oldest deposits, it occurs frequently in brackish and freshwater deposits (Duffin 1985, 2001; Cappetta 1987; Fischer 2008). There is the distinct possibility that many species of *Lissodus* were either partly or fully euryhaline but it is not known whether these taxa represent one or multiple lineages of non-marine forms (Maisey et al. 2004).

Lissodus was originally described on the basis of twenty articulated specimens of the type species *Lissodus africanus* (Broom, 1909) from the Middle Triassic (Anisian) of South Africa (Broom 1909; Brough 1935). These remains, together with two articulated specimens of *L. cassangensis* (Teixeira, 1956) from the Early Triassic of Angola (Antunes et al. 1990) and a few articulated but incomplete remains of *L. montsechi* (Gómez Pallerola, 1979) from the Early Cretaceous of Spain (Soler Gijón and Poyato-Ariza 1995) are the only articulated remains of the genus. All other material has been assigned to *Lissodus* based on isolated teeth, scales, and fin spines that are morphologically similar to the type species. Although dentition is the most important taxonomic criterion for systematic subdivision of the taxon *Lissodus* (Hampe 1996), there is the strong likelihood that some of the taxa that are solely based on isolated teeth would be highly vulnerable to synonymy without knowledge of the complete dental apparatus (Duffin 1985; Duncan 2004).

Duffin (1985, 2001) considered *Lonchidion* Estes, 1964, another small euryhaline hybodont from the Mesozoic, as a junior synonym of *Lissodus* because of the overall similarity of their teeth. Following his interpretation of the tooth morphology, currently 49 *Lissodus* species are recognised (Sardinian record here included), with about 67 further records not designated to species level (Fischer 2008). In a recent investigation, Rees and Underwood (2002) restored *Lonchidion* as a valid genus within the family Lonchidiidae Herman, 1977, with the genus *Lissodus* containing only 14 species, ranging from Early Triassic (Scythian) to late Early Cretaceous (Albian); all other records considered to be *Lissodus* by Duffin (2001) they referred to *Lonchidion* (13 species, Middle Triassic [Ladinian] to Late Cretaceous [Maastrichtian]); *Parvodus* (4 species, Middle Jurassic [Bathonian] to the Early Cretaceous [Valanginian]); *Hybodus* (2 species, Late Jurassic [Kimmeridgian], Early Cretaceous [Albian]); *Polyacrodus* (2 species, Early

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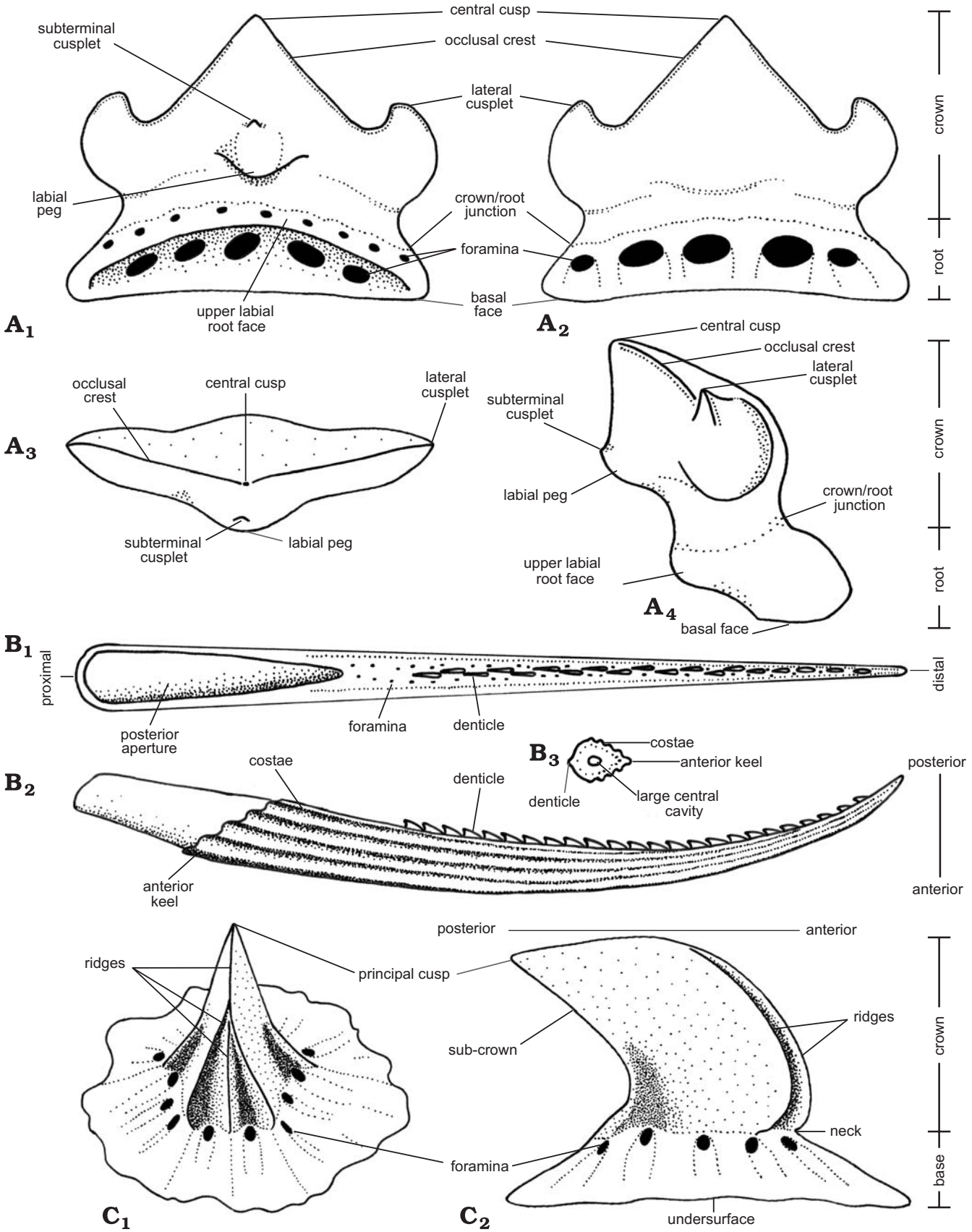

Fig. 3. Diagrammatic illustrations of teeth, fin spines and dermal denticles of *Lissodus sardiniensis* sp. nov. **A**. Tooth (following Duffin 1985), labial (A_1), lingual (A_2), occlusal (A_3), and lateral (A_4) views. **B**. Fin spine (modified from Schneider 1986), posterior (B_1), lateral (B_2) views, cross-section (B_3). **C**. Denticles (following Thies 1995), oblique anterior (C_1), and lateral (C_2) views.

Cretaceous [Valanginian, Berriasian]); *Vectiselachos* (1 species, Early Cretaceous [Berriasian–Aptian]); and *Steinbachodus* (1 species, Late Cretaceous [Cenomanian]). Furthermore, the Palaeozoic teeth assigned to *Lissodus* sensu Duffin (2001) and other authors (Gebhardt 1988; Soler-Gijón 1993, 1997; Hampe 1996) fall into two different morphological groups, which were left in open nomenclature by Rees and Underwood (2002). Recently, Rees (2008) has concluded that *Lissodus* should be left without family designation on the basis of its rather unique dentition and cephalic spine morphology.

Nevertheless, here we retain the view of Duffin (1985, 2001), placing the Sardinian specimens in the genus *Lissodus* because the revision of Rees and Underwood (2002) has only been convincingly applied to Mesozoic species (Duncan 2004; Fischer 2008).

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Euselachii Hay, 1902
Superfamily Hybodontoidea Owen, 1846
Family ?Lonchidiidae Herman, 1977
Genus *Lissodus* Brough, 1935

Type species: *Hybodus africanus* Broom, 1909, referred to the new genus *Lissodus* by Brough (1935); 21 ± complete articulated specimens from earliest Middle Triassic (Early Anisian), *Cynognathus* Assemblage Zone (Subzone B) of Bekker's Kraal, Beaufort series, South Africa.

Lissodus sardiniensis sp. nov.

Figs. 4–7.

Etymology: Named after the island of Sardinia (southern Italy), where the fossil site is situated.

Holotype: FG 589/T/027 a complete tooth with root (Fig. 4A).

Type locality: Northern slope of the Guardia Pisano hills, close to Gonnesa (Sulcis area, SW Sardinia, Italy).

Type horizon: Lacustrine limestone horizon at the top of lithofacies B, latest Carboniferous–earliest Permian (Gzhelian–Asselian), based on sporomorphs and radiometric dating.

Referred material.—Paratypes include teeth FG 589/T/028 (Fig. 4D), FG 589/T/031 (Fig. 4B), FG 589/T/059 (Fig. 5A), and FG 589/T/060 (Fig. 5B). Fin spine FG 589/F/001 (Fig. 7A). Dermal denticles FG 589/S/004 (Fig. 7F), FG 589/S/002 (Fig. 7J), FG 589/S/007 (Fig. 7M).

Additional material.—100 complete teeth and > 400 tooth fragments (mostly crowns), > 150 placoid scales and numerous fin spine fragments.

Diagnosis.—The favourable taphonomic situation enables fin spines and dermal denticles in addition to teeth to be included in the diagnosis of the new species of *Lissodus*.

Teeth minute, weakly heterodont, measuring from 0.34–1.31 mm in length. Central cusp prominent standing nearly upright in lateral teeth, becoming strongly labially inclined in mesial and posterior teeth; flanked by one pair of smaller lateral cusplets, clearly leaning toward the central cusp. In occlusal view, crown slightly asymmetric curving away from the mid-point to the labial edges in many teeth. Crown faces triangular-shaped and smooth, lacking vertical striations, accessory cusplets or nodes on the crown shoulders. Occlusal crest compressed into a rather sharp ridge with no crenulation. Labial peg (= labial buttress) usually prominent and not supported by a labial root buttress from below, often showing a tiny subterminal cusplet. Crown/root junction clearly incised around the whole tooth. Root lingually directed and less than one-half crown height but mostly longer than the crown. Root hybodontoid, showing three to five large, simple vascular foramina with anaulacorhize organisation. Central longitudinal pulp cavity situated high up at the crown/root junction. Upper labial root face usually with a single row of small foramina. Basal face crescent-shaped and strongly labially concave. Closest to the species are *Lissodus* cf. *zideki* (Soler-Gijón 1993) and *Lissodus lopezae* Soler-Gijón, 1997. However, the new material differs significantly from all other published Palaeozoic and Mesozoic species by the exhibition of a single prominent central cusp, which is flanked by one pair of curved, smaller lateral cusplets.

Fin spines gently curved posteriorly, ornamented with four well-developed smooth longitudinal costae on both sides. Anterior edge with a distinctive keel. Posterior side with a single median row of ventrally curved and weakly alternating hook-like denticles of about 0.5 mm in length. Cross section roughly ovoid of typical hybodontiform organisation. The overall appearance of the fin spines mostly resembles material of *L. lopezae* Soler-Gijón, 1997, but differs in the number of denticles.

Dermal denticles vary in shape and size forming distinctive scale morphotypes, most of hybodontoid non-growing type. Crown single to multicuspid; in most scales pointed posteriorly and ornamented with longitudinal ridges on the crown surface. Average crown height 0.5 mm; length varies from 0.5–1.34 mm. Sub-crown smooth; in some specimens a mesial ridge can be recognised. No distinct neck between base and crown. Base in central position, and wider than the crown base to all margins. Undersurface of base (= basal plate) slightly curvate with a large central pulp canal opening. Base outline circular with crenulated margin (multipetaloid), 0.5–1.0 mm in diameter. The denticle assemblage is most similar to Palaeozoic hybodont material described by Gebhardt (1986).

Description of the teeth.—Three morphotypes can be distinguished, which are linked by a gradual transition:

Tooth morphotype I (Fig. 4): The shape and size of teeth in morphotype I vary considerably but are united into one morphotype because of the many transitions between them. The length along the occlusal crest ranges from 0.55– 0.92 mm. The central cusp is prominent but often appears low because of a strong labial inclination in most specimens (Fig. 4G, I) and so the crown of most specimens curves away occlusally from the midpoint to the labial edges (Fig. $4A_2$, B_2, C_2, D_2). The lateral cusplets are one-third to one-half of the central cusp height with steeply dipping sides (Fig. $4A_1$, D_1, E, F, H); they are pointed and tend to lean toward the cen-

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tral cusp (Fig. $4A_1$, B_3, E, F, H). The occlusal crest is moderate, but in some specimens strong on the lateral cusplets (Fig. $4D_3$–F). The labial peg is prominently developed (Fig. $4A_2$, D_2, J), protruding aborally (Fig. $4A_1$, B_1, C_1, I), and in most specimens carries a tiny subterminal cusplet (Fig. $4A_1$, G–J). A lingual peg is occasionally developed (Fig. $4C_3$, E, F). The crown/root junction is moderately incised. The root is flat, slightly longer than the crown (Fig. $4B_3$, E, I) and less than half the crown height. The lingual root face shows three to five simple vascular foramina (Fig. $4B_3$, C_1, D_3–F) and the labial side has a row of up to seven smaller foramina (Fig. $4A_1$, D_1). This morphotype represents ~75% of all teeth and is the most common tooth-type.

Tooth morphotype II (Fig. 5A–H): The length along the occlusal crest ranges from 0.34–0.54 mm. The sharp central cusp is prominent (Fig. $5A_3$, C, D, G) and strongly labially inclined in most specimens (Fig. $5A_1$, B_1, E) so that the crown is distinctly asymmetrical occlusally (Fig. $5A_2$, B_2). The lateral cusplets are slightly rounded (Fig. 5E, F), most lean toward the central cusp and half the height of the central cusp. The occlusal crest is moderate (Fig. 5F, G) and the labial peg is prominently developed (Fig. 5H) with a minute subterminal cusplet. In total, the whole shape of the crown resembles a spade, supported by a strongly incised crown/root junction (Fig. 5C, G). The root is normally half the crown height and noticeably shorter than the crown (Fig. $5B_1$). Teeth of this morphotype have the highest coronal profile. On the lingual root face up to five simple vascular foramina are present (Fig. 5F–H) and there are up to seven smaller foramina arranged in a row on the upper labial side (Fig. $5A_1$). This morphotype represents ~20 % of all teeth and is the second most common tooth-type.

Tooth morphotype III (Fig. 5I–N): The length along the occlusal crest ranges from 1.01–1.31 mm. The crown is elongate and relatively small. The central cusp is prominent and the lateral cusplets are well rounded perhaps as a consequence of abrasion (Fig. 5K, M, N). The lateral cusplets lean toward the central cusp (Fig. 5L) and are one half of its height. In occlusal view the central cusp lies more or less in a line with the lateral cusplets. The occlusal crest is strong and the labial peg is moderate developed (Fig. 5I). The crown/root junction is incised. The root is flat measuring less than half the crown height but is somewhat longer than the crown. On the lingual root face there are five vascular foramina (Fig. 5J) and on the labial side up to 11 small foramina are present in a line (Fig. 5I, K). This is the least common morphotype represents ~5% of all teeth. Only a few complete teeth have been found: most specimens are crowns or half teeth.

Tooth histology (Fig. 6): Sectioned tooth crowns and complete teeth from probably mesial or anterolateral positions revealing a layer of single crystallite enameloid (SCE) up to 40 μm thick (Fig. 6), and especially well developed on the labial crown side (Fig. 6B–D). Orthodentine is developed beneath the enameloid in the crown and contains long, sub-parallel, sometimes branched tubules. The dentine tubules are evenly distributed over the crown and show a weak fan-shaped radiation from the central cavity (Fig. 6D). The central pulp cavity is clearly developed (Fig. 6B), now filled with sediment (Fig. 6A). All the teeth of *L. sardiniens* sp. nov., which have been examined for histology show a distinct orthodont internal structure (sensu Reif 1973).

Description of the fin spines.—(Fig. 7A–E) Fin spines are only preserved as many small fragments, measuring from 0.30–7.0 mm in length, 1.30 mm in width and 0.50–1.50 mm in height. Some larger specimens possess a gently curved posterior face (Fig. 7A). The lateral faces of the spines are well ornamented with continuous smooth longitudinal costae (Fig. 7A–E). Normally four costae are present laterally (Fig. 7D); the more proximal part of the spine is unknown. The intercostal spaces are comparatively wider in the anterior part of the spine (Fig. 7C). Irregular foramina lie between the costae (Fig. 7C). Neither costal bifurcation nor anastomosis are observed. Toward the spine tip, the number of costae decreases to three. One strong costa forms a keel along the anterior border of the spine (Fig. 7D, E).

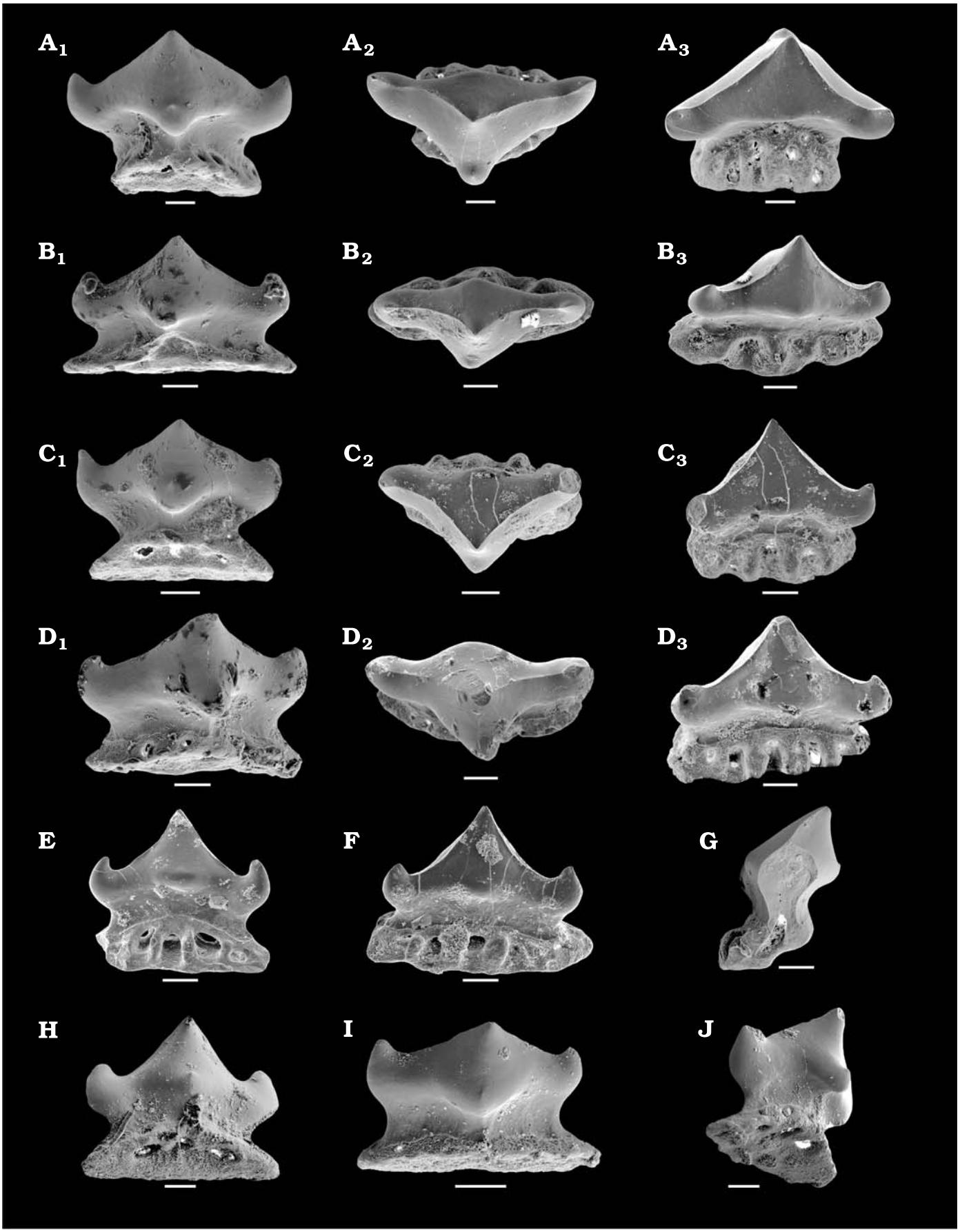
Hooked denticles are arranged in a single median row along the posterior face of the spine (Fig. 7A–C). The denticles are sharp, laterally compressed, longer than high and possess a strong dorsal crest (Fig. 7C). The length of each denticle is about 0.50 mm and the width is about 0.25 mm. Many fragments show a tight array of denticles, which suggests a closed denticle row on a complete fin spine. An exception is provided by FG 589/F/005 (Fig. 7B), which shows a small space between the single denticles. The denticles are weakly arcuate laterally and slightly displaced alternately to the left and right of the midline. Toward the spine tip the height of the denticles decreases noticeably. There would be approximately 20 denticles per cm in a complete fin spine. The posterior spine face also displays two smooth, small costae and small foramina marginally.

The subovoid cross section shows an outer, cavernous, highly vascularised layer of osteodentine, an inner lamellar layer with few canals and a large central cavity (Fig. 7D, E).

Description of the dermal denticles.—(Fig. 7F–O) Three basic morphotypes can be distinguished amongst the scales:

Scale morphotype 1 (Fig. 7F–I): These are non-growing scales, measuring up to 1.34 mm in length and 0.89 mm in height. The crown is centrally placed, upright with a single central cusp, which is usually cone- or dome-shaped, and in

Fig. 4. Teeth of hybondontoid shark *Lissodus sardiniensis* sp. nov. Morphotype I, Gzhelian–Asselian of Guardia Pisano, Sardinia, Italy. **A**. Holotype FG 589/T/027, labial (A_1), occlusal (A_2), and lingual (A_3) views. **B**. Paratype FG 589/T/031, labial (B_1), occlusal (B_2), and lingual (B_3) views. **C**. FG 589/T/032, labial (C_1), occlusal (C_2), and lingual (C_3) views. **D**. Paratype FG 589/T/028, labial (D_1), occlusal (D_2), and lingual (D_3) views. **E**. FG 589/T/023, lingual view. **F**. FG 589/T/025, lingual view. **G**. FG 589/T/010, lateral view. **H**. FG 589/T/009, labial view. **I**. FG 589/T/018, labial view. **J**. FG 589/T/019, oblique labial view. Scale bars 100 μm. →



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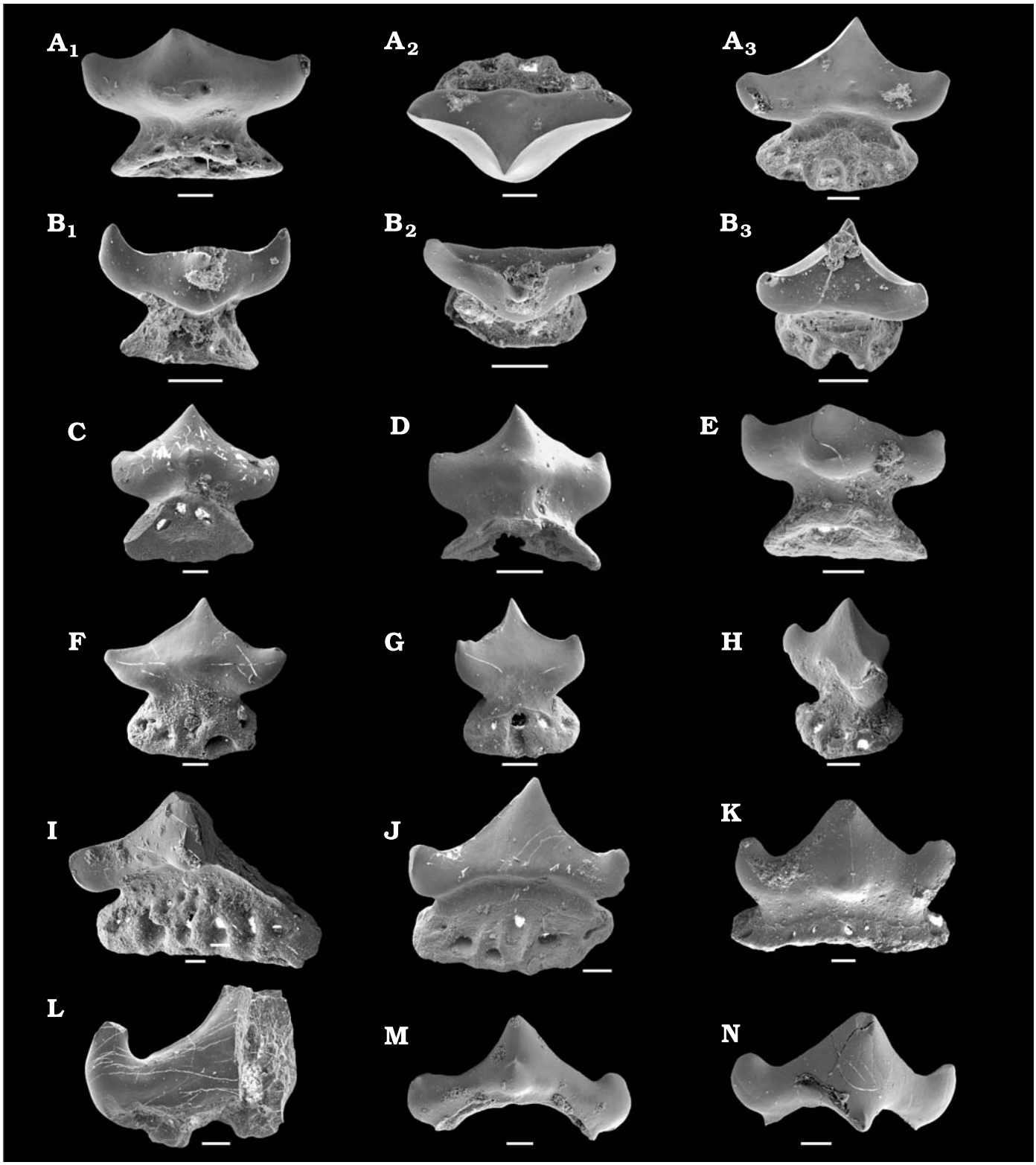

Fig. 5. Teeth of hybondontoid shark *Lissodus sardiniensis* sp. nov. Morphotype II (**A**–**H**) and morphotype III (**I**–**N**), Gzhelian–Asselian of Guardia Pisano, Sardinia, Italy. **A**. Paratype FG 589/T/059, labial (A_1), occlusal (A_2), and lingual (A_3) views. **B**. Paratype FG 589/T/060, labial (B_1), occlusal (B_2), and oblique lingual (B_3) views. **C**. FG 589/T/051, labial view. **D**. FG 589/T/052, labial view. **E**. FG 589/T/053, labial view. **F**. FG 589/T/058, lingual view. **G**. FG 589/T/055, lingual view. **H**. FG 589/T/056, lingu-lateral view. **I**. FG 589/T/062, labial view. **J**. FG 589/T/066, lingual view. **K**. FG 589/T/061, labial view. **L**. Crown FG 589/T/065, lingual view. **M**. Crown FG 589/T/064, labial view. **N**. Crown FG 589/T/063, labial view. Scale bars 100 μm.

some cases more thorn-like (Fig. 7G) and slightly curved posteriorly. The crown surface is ornamented with numerous strong vertical ridges that meet at the crown apex (Fig. 7F–I). In specimen FG 589/S/004 (Fig. 7F) the ridges bifurcate

twice or more. A distinct neck is missing in the flat dome-shaped scales but developed in more thorn-like specimens. The base is wider than the crown to all margins and the outline is multipetaloid. The undersurface of the base is slightly concave, and the surface carries radial ridges, which are partial continuations of the crown ridges; numerous foramina for basal canals occur on all sides. This scale-type comprises less than 15% of the total dermal denticle assemblage.

Scale morphotype 2 (Fig. 7J–L): Like morphotype 1, these are non-growing scales, measuring up to 0.73 mm in length and 0.54 mm in height. The upright crown is lanceolate, strongly compressed laterally, and the posterior cusp is sharply curved backwards so that in lateral view it appears hook-shaped (Fig. 7J). A sharp median crest bifurcates the anterior rim resulting in a crown ornament with three strong vertical ridges (Fig. $7K_2$). Laterally, on the crown surface of some specimens further moderate ridges are developed. The crown is situated centrally on a large base (Fig. 7K). The sub-crown is smooth and restricted laterally by a ridge on each side. In some specimens a mesial ridge can be recognised on the sub-crown. The neck is not very well developed. The base is wider than the crown to all margins (Fig. $7K_2$), and the undersurface is slightly concave from below. The outline of the base is multipetaloid and its surface carries radial ridges, which are partial continuations of the crown ridges. Numerous foramina occur on all sides of the scale (Fig. 7K). A small number of specimens (~5% of all scales) present the basal fusion of two unicuspid scales of this morphotype forming a multicuspid scale (Fig. 7L). This hook-like morphotype represents ~70% of all scales and is the most common scale-type in the microfossil sample.

Scale morphotype 3 (Fig. 7M–O): These are growing scales, measuring up to 0.60 mm in length and 0.74 mm in height. The crown stands upright, is very elongate laterally but very thin antero-posteriorly (Fig. $7M_1$, N), exhibiting several strong to moderate ridges on the convex anterior side (Fig. 7M–O) whereas the concave posterior side is completely smooth. Up to six posterior sharp cusps are developed in this complex scale-type. The neck is moderate and vascular canals are visible near the crown/base junction (Fig. 7N). The base is poorly preserved in most specimens, and wider than the crown. The basal surface outline is multipetaloid to cycloid, and radial ridges on the surface are weakly developed. The undersurface of the base is strongly concave with a central pulp cavity. This scale-type forms ~15% of the total of scales in the sample.

Discussion of the teeth.—The teeth from Guardia Pisano show the presence of some diagnostic features of the genus *Lissodus* (Duffin 1985; Rees and Underwood 2002): a crown with a triangular contour, a well developed central cusp, flanked by smaller lateral cusplets, a moderate to strong occlusal crest, a strong labial peg, a lingually inclined root that is narrower than the crown, and a single row of small foramina near the crown/root junction.

In addition, the teeth also share some diagnostic features of *Lonchidion* as determined by Rees and Underwood (2002):

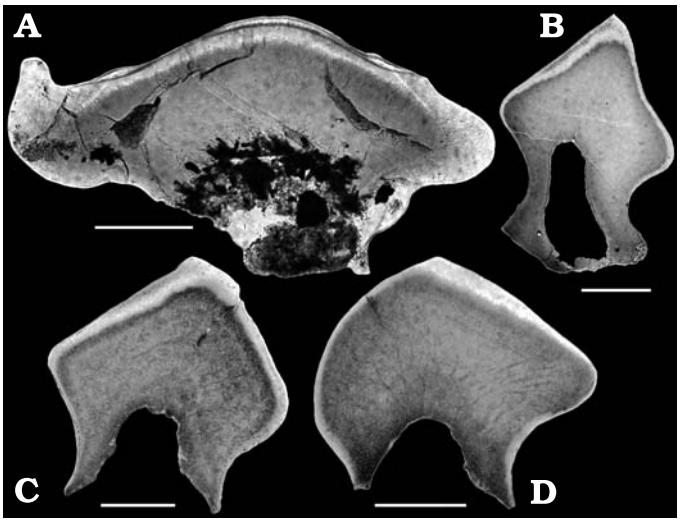

Fig. 6. Thin sections of teeth of hybondontoid shark *Lissodus sardiniensis* sp. nov. shown under ordinary light, Gzhelian–Asselian of Guardia Pisano, Sardinia, Italy. **A**. FG 589/T/033 complete tooth. **B**. FG 589/T/034 complete tooth. **C**. FG 589/T/035 tooth crown. **D**. FG 589/T/037 tooth crown. Scale bars 100 μm.

the teeth are extremely gracile, only 0.34 mm long in some specimens, the root is generally wider than the lowermost part of the crown with a strongly concave labial side.

Altogether, the character combination found in the teeth from Guardia Pisano most clearly resembles in certain respects that of the Palaeozoic teeth belonging to *L.* cf. *zideki* (Soler-Gijón 1993), *L. lopezae* Soler-Gijón, 1997, *L. lacustris* Gebhardt, 1988, *L.* sp. (subtype no. 107 of Tway and Zidek 1983), *L.* sp. (NM) (Hampe 1996), and *L. zideki* (Johnson, 1981) because of the symmetrical, mostly non-ornamented crown with a distinctive occlusal crest, triangular outline in occlusal view and pointed but prominently labially inclined central cusp. All these taxa are from the Late Palaeozoic and assigned to *Lissodus* after Duffin (1985) but classified as "Palaeozoic genus 1" in open nomenclature by Rees and Underwood (2002). This arrangement into a separate group besides *Lissodus* was justified by the specific character combination of the teeth ("… the labially inclined cusps and the lack of lateral cusplets, in combination with the heterodonty pattern ..."), which would be atypical for the morphological range of *Lissodus* according to Rees and Underwood (2002: 477). However, an inclined prominent cusp is not restricted to these forms, as it is also known from Mesozoic species such as *Lonchidion selachos*. Moreover, not all of the teeth of these Palaeozoic species lack lateral cusplets—see for instance, *L.* cf. *zideki*, *L. zideki*, and *L.* sp. (subtype no. 107 of Tway and Zidek 1983). Altogether, the separation of Palaeozoic species as "Palaeozoic genus 1" is not convincing. Therefore, the former assignment of these species to *Lissodus* by Duffin (1985) and subsequent authors is retained and the Sardinian specimens are attributed to *Lissodus*.

The Palaeozoic species closest to *L. sardiniensis* sp. nov. are *L.* cf. *zideki* (Soler-Gijón 1993) and *L. lopezae* Soler-Gijón, 1997 from the Late Carboniferous (Stephanian

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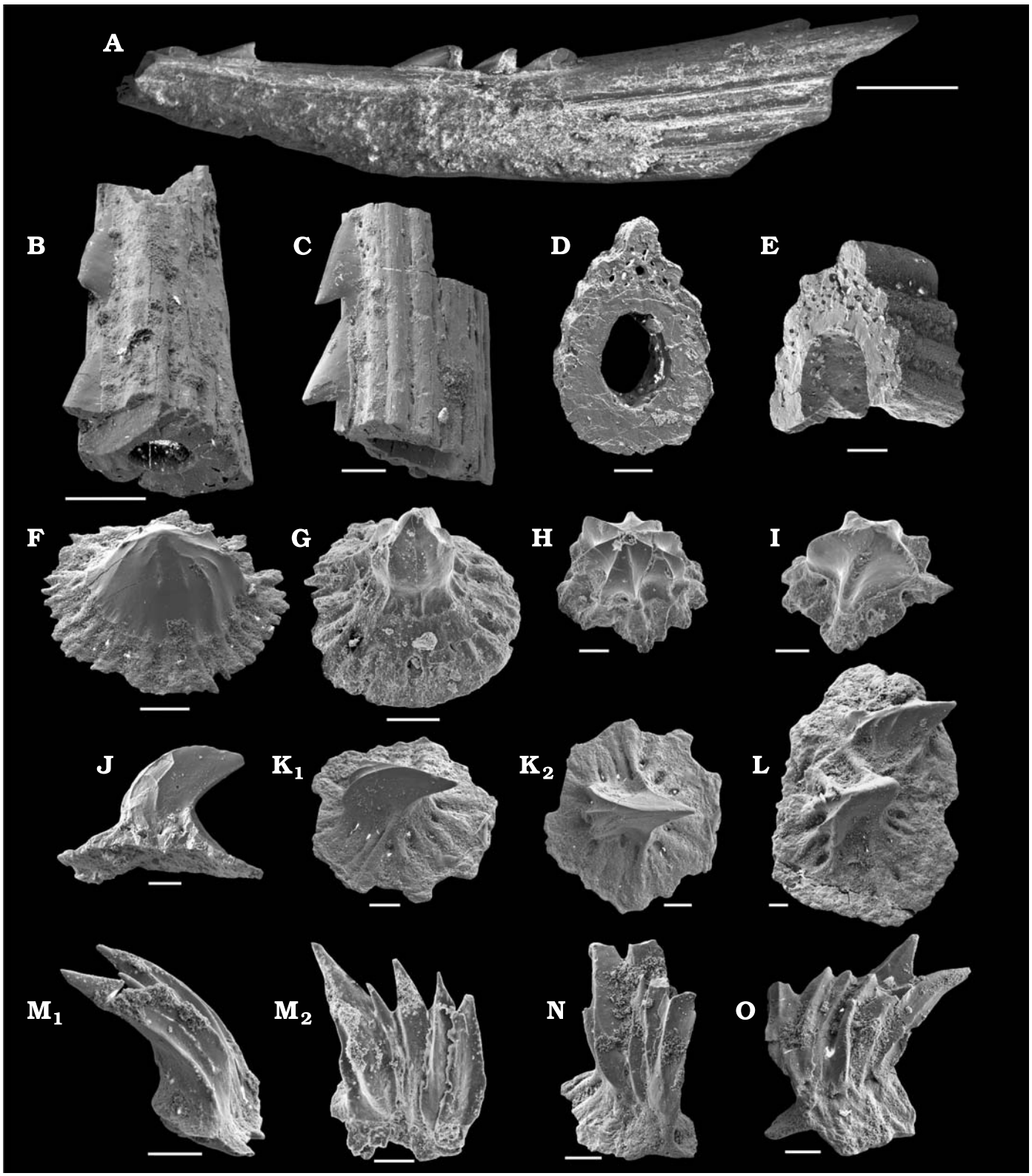

Fig. 7. Spine fragments (**A**–**E**) and dermal denticles: morphotype 1 (**F**–**I**), morphotype 2 (**J**–**L**), and morphotype 3 (**M**–**O**) of hybondontoid shark *Lissodus sardiniensi* sp. nov., Gzehlian–Asselian of Guardia Pisano, Sardinia, Italy. **A**. FG 589/F/001, lateral view. **B**. FG 589/F/005, lateral view. **C**. FG 589/F/002, lateral view. **D**. FG 589/F/003, cross-section with anterior side above. **E**. FG 589/F/004, cross-section of the anterior side with the keel. **F**. FG 589/S/004, oblique lateral view. **G**. FG 589/S/009, oblique lateral view. **H**. FG 589/S/010, oblique lateral view. **I**. FG 589/S/011, oblique lateral view. **J**. FG 589/S/002, lateral view. **K**. FG 589/S/001, oblique lateral (K_1), dorsal (K_2) views. **L**. coalesced denticle FG 589/S/003, oblique dorsal view. **M**. FG 589/S/007, lateral (M_1), anterior (M_2) views. **N**. FG 589/S/006, oblique lateral view. **O**. FG 589/S/005, anterior view. Scale bars: A, 1 mm, B–G, 300 μm, H–O, 100 μm.

C = Gzhelian–Asselian) of Puertollano in central Spain. Teeth of these three species are tiny, overlapping in size from *L.* cf. *zideki* (0.31–0.62 mm) over *L. sardiniensis* sp. nov. (0.34–1.31 mm) to *L. lopezae* (0.95–1.19 mm). They also share a tiny subterminal cusplet on the labial peg, although the Spanish species lack well-defined lateral cusplets. Furthermore, nodes and a longitudinal ridge along the labial crown shoulder are present in both Spanish species but are absent in *L. sardiniensis* sp. nov.

Lissodus lacustris Gebhardt, 1988 from the Late Carboniferous (Stephanian C) of Germany differs from the Sardinian specimens in the presence of nodes on a clearly crenulated crown shoulder, weak or absent lateral cusplets and a labial root buttress.

Lissodus zideki (Johnson, 1981) from the late Early Permian (late Artinskian-Kungurian) of Texas, USA. differs from *L. sardiniensis* sp. nov. with incipient or absent lateral cusplets, occasionally labial nodes and size (1.5–2.0 mm).

Lissodus sp. (subtype no. 107 of Tway and Zidek 1983) from the Late Carboniferous (Stephanian C) of Kansas differs in possessing incipient cusplets and lacks a subterminal cusplet on the labial peg.

Lissodus sp. (NM) (Hampe 1996) from the Early Permian (Asselian) of Germany differs in possessing a poorly developed labial peg, a vertical ridge from the central cusp to the labial peg, the absence of lateral cusplets and a mesiodistal length of 2.0–4.0 mm.

The Mesozoic species closest in morphology to *L. sardiniensis* sp. nov. is *Lonchidion selachos* Estes, 1964 from the Late Cretaceous (Campanian–Maastrichtian) of Wyoming, USA. The two species share a non-ornamented crown, a tiny subterminal cusplet on the labial peg, and a labially inclined central cusp. In addition, some symphyseal teeth show the same triangular shape of the crown with a prominent cusp and one pair of curved lateral cusplets (Estes 1964: fig. 2b). However, only some symphyseal teeth of *Lonchidion selachos* develop this distinctive shape, whereas it is a universal feature in *L. sardiniensis* sp. nov.

Histologically, teeth with one layer of SCE belong to the "α tooth type" of Reif (1973). The fan-shaped radiation of dentinal tubules from the central cavity is similar to structures described in teeth of *Lonchidion* by Estes (1964: fig. 2d); see also Patterson (1966: pl. 5: 1), and Heckert et al. (2007). The absence of an osteodentine core in any of the available teeth distinguish the Sardinian teeth from those of *Lissodis zideki* (Johnson, 1981), and *L. angulatus* Stensiö, 1921 from the Lower Triassic of Spitsbergen. The latter show two types of histology (osteodentine- and orthodentine type) within one taxon (Błażejowski 2004) whereas *L. sardiniens* sp. nov. is exclusively orthodont.

In spite of all the similarities with Palaeozoic and also Mesozoic species of *Lissodus* and *Lonchidion*, the teeth from Guardia Pisano differ significantly from all other published species especially in one characteristic feature. Exclusively *L. sardiniensis* sp. nov. alone possesses a single prominent central cusp, which is flanked by one pair of curved, smaller lateral cusplets in all of its teeth. On the basis of a hypothetical reconstruction of a dentition of *L. nodosus* (Seilacher, 1943) by Duffin (1985: fig. 12) the Sardinian morphotype I probably represents a mesial to anterolateral position whereas morphotype II being derived from a symphyseal position. The small root in the latter suggests that they were most likely not posteriors because of the crushing forces involved at the posterior end of the jaw in durophagous sharks. Morphotype III most likely occupied a lateral position because of its size and the more elongate shape.

Discussion of the fin spines.—The histology of the fin spine fragments from Guardia Pisano corresponds exactly to that described for hybodontiform fin spines by Maisey (1978). Unfortunately, isolated dorsal fin spines of hybodont sharks can only be assigned to the generic level. Applying the argument of Milner and Kirkland (2006) fin spines of *Lissodus* are ornamented laterally by costae, whereas those of *Lonchidion* are characterised by smooth lateral sides, with the exception of *Lonchidion humblei* Murry, 1981, which has costae. For that reason Milner and Kirkland (2006) suggested that *Lonchidion humblei* should be assigned to a taxon other than *Lonchidion*; in our opinion this should be referred to *Lissodus*. The Sardinian spine material can only be compared with material of Palaeozoic and Mesozoic hybodontoid species showing laterally ornamentation.

Spines of *L. africanus* (Broom, 1909) from the Early Anisian of South Africa (Brough 1935), and *L. cassangensis* (Teixeira, 1956) from the Scythian of Angola (Antunes et al. 1990) bear a double row of denticles along each posterolateral margin, in contrast to the Sardinian spine fragments. Furthermore, the African species are ornamented with six to seven costae whereas in the Sardinian fragments no more than four costae are present.

Comparison with *Lissodus* (*Lonchidion*) *humblei* Murry, 1981 from the Late Triassic (Carnian–Rhaetian) of the southern USA reveals differences in the number of costae with up to 12 at the proximal end of the spine and the development of two parallel denticle rows proximally in the American fin spines.

Dorsal fin spine material of *Lonchidion* sp. from the British Wealden (Tithonian–Berriasian) (Patterson 1966) shows many similarities with the Sardinian fragments. Up to five costae are present, showing no bifurcation or anastomosis and a single median row of hook-like denticles is also developed. Differences include the wider array of single denticles in the median row and a length of about 70 mm, which most likely was not reached by the Sardinian specimens.

Isolated fin spines from the Late Carboniferous (Stephanian C) of the Saale Basin, Germany, which were first questionably assigned to *Limnoselache vincinalis* by Schneider (1986: figs. 2a–c, pl. 1: 6–8) and subsequently attributed to *Lissodus lacustris* by Soler-Gijón (1997: 162), show an anterior keel along the entire spine length, and six smooth longitudinal costae laterally, of which only two to three reach the distal end of the spine. Bifurcation or anastomosis is ab-

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sent, a median denticle row is present and the cross section is similar to that described for *L. sardiniensis* sp. nov. Differences include a higher number of lateral costae, an average number of six denticles per centimetre, and the wider distance between the single denticles.

Soler-Gijón (1997: fig. 6, pl. 2: 9) described spines from the Late Carboniferous (Stephanian C) of the Puertollano Basin, Spain, which he assigned to *L. lopezae*. These correspond to the Sardinian remains in nearly all morphological criteria except the number of denticles per centimetre (six in *L. lopezae*), which in turn correlates with the spine material described by Schneider (1986) probably belonging to *L. lacustris* based on associated teeth from the same horizon.

Because of the co-occurrence in Sardinia hybodontiform spine fragments and teeth from the same horizon, and the absence of any other hybodontiform shark remains in these beds, the most parsimonious explanation is that both belong to the same species. Based on the size of the single fragments the original fin length can only be estimated at 40–50 mm, corresponding roughly to the size of the spine material of the other Palaeozoic *Lissodus* species described by Schneider (1986) and Soler-Gijón (1997). Neither is it easy to determine how many fin spines are represented in the collection, although the huge number of fragments indicates the presence of more than one original spine. Differences in size of the fragments or in the distance between denticles possibly represent individual variation. Furthermore, it is possible that some spines are from juveniles and others from adults. However, this question cannot be answered from the available isolated material.

Discussion of the dermal denticles.—Morphotype 1 is of strong hybodontoid affinity. It agrees well morphologically with some cone-shaped scales from the lower jaw and the roof of the mouth cavity of *Hybodus delabechei* Charlesworth, 1839 from the Early Jurassic (Sinemurian) of England (Reif 1978: fig. 2a) as well as with unidentified scales of "hybodontiform morphotype 1" from the Late Jurassic (Kimmeridgian) of northern Germany (Thies 1995: fig. 4a–d). Maisey (1983: fig. 23c, d) found such scales in the head region of *Hybodus basanus* from the Lower Cretaceous of England. Furthermore, Delsate et al. (2002: figs. 17-1b, pl. 10a) described similar scales of a undetermined "hybodontiform type 2, group a" from the Early Jurassic (Middle Hettangian) of South Belgium. Therefore, the record from Guardia Pisano extends the record of scales of this morphotype from the genus *Hybodus* as questioned by Thies (1995), to *Lissodus*. Moreover, Schneider (1986: pl. 3: 6, 8) assigned scales from the Late Carboniferous (Stephanian C) of the Saale Basin, Germany to *Limnoselache vicinalis* (= *Sphenacanthus* Soler-Gijón 1997), which show a similar crown shape but a convex basal plate in lateral view. The same scale type from the same locality was also described by Gebhardt (1986: pl. 1: 3) as "type H d2", there with a more hook-like shape in lateral view. From the Early Permian of the middle and southern Urals Ivanov (2005: fig. 5J) described a "*Petrodus*" type denticle that shares this morphology. Duffin (1985) reported entirely simple, stud-like scales with upright crowns from the squamation of *L. africanus*, which are similar to morphotype 1. Duffin (1993: fig. 14d, e) described simple, stud-like scales with bifurcate vertical ridges of an undetermined "type 2". Rees (2002: fig. 9.1–3) described similar hybodontoid scales from the earliest Cretaceous Vitabäck Clays of southern Sweden as "morphotype 1". This simple hybodontoid scale morphotype (Reif 1978) is also known in all articulated hybodont specimens of the Jurassic and Cretaceous (Duffin 1993).

Morphotype 2 is also considered to be of hybodontoid affinity. It is morphologically similar to thorn-shaped scales of *Hybodus delabechei* Charlesworth, 1839 from the Early Jurassic (Sinemurian) of England (Reif 1978: fig. 2d) as well as with some unidentified scales of the "hybodontiform morphotypes 2 and 3" from the Late Jurassic (Kimmeridgian) of northern Germany (Thies 1995: fig. 4f–i). It also resembles specimens described from the Early Jurassic (Middle Hettangian) of southern Belgium from undetermined "hybodontiform scale-type 2, group b" by Delsate et al. (2002: fig. 18, pl. 10c). Hampe (1996: figs. 7a–c) described as "morphotype 2A" similar lanceolate, posteriorly recurved and keeled scales of *L.* sp. (NM) from the Early Permian (Lower Rotliegend) of Germany. Other unicuspid denticles with lanceolate cusps curved posteriorly are known from the Late Carboniferous (Stephanian C) of the Saale Basin in Germany called "type F d3" and "d6" by Gebhardt (1986: pl. 3: 1,4); these undetermined dermal denticles are from the same horizon as *L. lacustris* Gebhardt, 1988 and are very similar to morphotype 2 material from Sardinia in showing a smooth crown surface with strong anterior ridges and a median posterior crest. The only difference is the narrow basal plate in the German material. Rees (2002: fig. 9.4) documented a similar scale as "morphotype 3" from the Cretaceous of southern Sweden. In Recent sharks, *Squalus acanthias* possesses similar scales with a single lanceolate and backwards-curved crown and a polygonal base in the posterior part of the oral cavity (Reif 1985: pl. 8, M2). Multicuspid scales similar to the fused specimens of morphotype 2 are described by Reif (1978: fig. 8d, e) for *Hybodus delabechei* and Reif (1985: pl. 15) for placoid scales of the Recent shark *Echinorhinus brucus*. These primary unicuspid scales become fused at their bases in the case of irregular spacing during formation-time. Such scales cannot be regarded as growing scales (Reif 1978). The frequency of scales of morphotype 2 in the microfossil sample (~70% of all scales) probably indicates that this scale-type was the principal squamation morphotype of *L. sardiniensis* sp. nov. covering the bulk of the shark's body.

Morphotype 3 strongly resembles a scale referred to *Ctenacanthus* from the Late Permian of Greenland (Reif 1978: fig. 1e). However, growth rings on the lower side on the base are not recognisable in our morphotype 3. Mader and Schultze (1987: fig. 4a, b) described two different undetermined scales from the Early Carboniferous (Viséan) of western Germany showing a serrated crown of several separated ridges. Gebhardt (1986: pl. 1: 2) described similar scales from the Stephanian Wettin Subformation of Germany

as "type H d1", which possess at least two lanceolate ridges forming a multicuspid shape but with a more cylindrical crown. Moreover, Soler-Gijón (1997: pl. 2: 1) showed a multicuspid scale from the Late Carboniferous (Stephanian C) of Spain, which he assigned to the ?ctenacanthid *Sphenacanthus carbonarius*, and which resembles the rake-like shape, but with a convex basal undersurface and a round crown base. Masson and Rust (1983: fig. 7) described an undetermined elasmobranch denticle from the Late Pennsylvanian Morian Group of the Sydney Basin, Nova Scotia, Canada, which resembles the multicuspid rake-shape of morphotype 3 in lateral view. Ginter and Sun (2007: fig. 13E_1, E_2) displayed such scales from the Early Carboniferous (Tournaisian) of Muhua, southern China, identifying them as ctenacanth scales. A scale assemblage from the Early Permian of the Middle and Southern Urals also contains a similar scale, described as "*Listracanthus*" denticles by Ivanov (2005: fig. 5L). Finally, Johns (1996: pl. 2: 7) created a key to Triassic elasmobranch scales from north-eastern British Columbia, Canada, which contains a similar scale-type with lanceolate and inclined crown with multiple paired ridges. Interestingly Johns (1996) assigned this scale-type to the hybodontoid scale morphotype after Reif (1978). The same assignment was done by Rees (2002) with a similar shaped "morphotype 6" from the Cretaceous of southern Sweden.

The assignment of morphotype 3 is difficult. Although these scales are most similar to the ctenacanthid morphotype of Reif (1978), no other remains of ctenacanthid sharks were found in the Sardinian samples. Furthermore, the scales described by Gebhardt (1986) are from the same stratigraphic level as remains of *L. lacustris* Gebhardt, 1988, and the scales described by Soler-Gijón (1997) are from the same stratigraphic level as remains of *L. lopezae* Soler-Gijón, 1997. It seems to be a strong possibility that the scales from Germany and Spain in fact belong to *Lissodus.* This characteristic scale-morphotype probably represents a primitive complex scale form that occurred since the Devonian in ctenacanthid (Basden et al. 2006: fig. 11) as well as in hybodont sharks but because of the disarticulated hybodontoid remains especially from the Palaeozoic this cannot be verified.

Assignment to generic or even species level based on disarticulated scales is extremely difficult because most fossil and also Recent sharks show heterosquamation (Reif 1985; Johns 1996). The scale morphology varies greatly from one elasmobranch family to another, from one genus to another within the same family and also within one species according to ontogenetic stage, region of the body, between specimens of different size and even between different gender (Reif 1974; Cappetta 1987; Kemp 1999). So far placoid scales possess low taxonomic significance because of this wide variability (Reif 1985; Thies 1995; Duffin 1999). Because of this and the poor record of scales from articulated squamations from a single elasmobranch species fossil shark scales can often only be assigned to the familial level. However, the co-occurrence of undoubtedly hybodontiform scales and teeth from the same stratigraphical horizon of Guardia Pisano supports the assignment to the same taxon as above for the spines.

After comparison with other described material, the scale assemblage from Guardia Pisano shows greatest affinity with specimens described by Gebhardt (1986) from the Late Carboniferous (Stephanian C) of the Saale Basin, Germany, which is also the type locality of *L. lacustris* Gebhardt, 1988. Because the scales are disarticulated, the position on the shark's body is only generally determinable.

Based on the above discussion the material from the Gzhelian–Asselian of the Guardia Pisano Basin of Sardinia is referred to the new species *Lissodus sardiniensis* sp. nov., encompassing teeth, fin spines, and dermal denticles.

Palaeoecology

The limestone horizon of Guardia Pisano with its vertebrate assemblage is undoubtedly of non-marine origin, because of the geological setting, facies architecture (Pittau et al. 2002; Barca and Costamagna 2006; Ronchi et al. 2008), and the absence of marine fossils. The latter is of course negative evidence but because of the preservation potential of the Guardia Pisano limestone for any kind of apatitic material, such as vertebrate remains, for primary aragonitic shells as in gastropods, and for chitin as in ostracods, the absence of indicative marine fossils is not due to taphonomic bias. Both fossil content and the lithofacies pattern show that this is a limestone definitely deposited in a non-marine setting in the Peri-Tethys realm based on the palaeogeography with no marine influence. This is in good agreement with the criteria for recognising freshwater environments by Gray (1988). Moreover, it contradicts the assumption by Schultze and Soler-Gijón (2004) and Schultze (2009) who are regarding all European Permocarboniferous basins as marginal marine environments with a marine influence. The occurrence of sharks itself does not confirm a marine signal or adjacent marine areas, because the fact that living sharks are marine does not imply that all fossil sharks were marine. Deducing the behaviour of extinct taxa from extant relatives seems to be a weak argument (Gray 1988; Poyato-Ariza et al. 1998; Schultze 2009), especially for geologically old forms. Hybodont sharks as the extinct sister group of neoselachians (Maisey et al. 2004) clearly indicate behaviour that is unknown in extant relatives. Whereas no Recent oviparous shark is known to deposit its egg capsules in non-marine environments (Schultze and Soler-Gijón 2004) hybodont egg capsules of the *Palaeoxyris*-type are known from doubtless freshwater deposits (e.g., Schneider and Reichel 1989; Axsmith 2006; Fischer et al. 2007). Furthermore, egg capsules, as well as remains of juvenile to adult individuals of xenacanthids in fluvial and lacustrine environments are documented (Schneider and Reichel 1989; Schneider and Zajíc 1994; Schneider 1996) demonstrating the performance of complete life cycles in non-marine realms.

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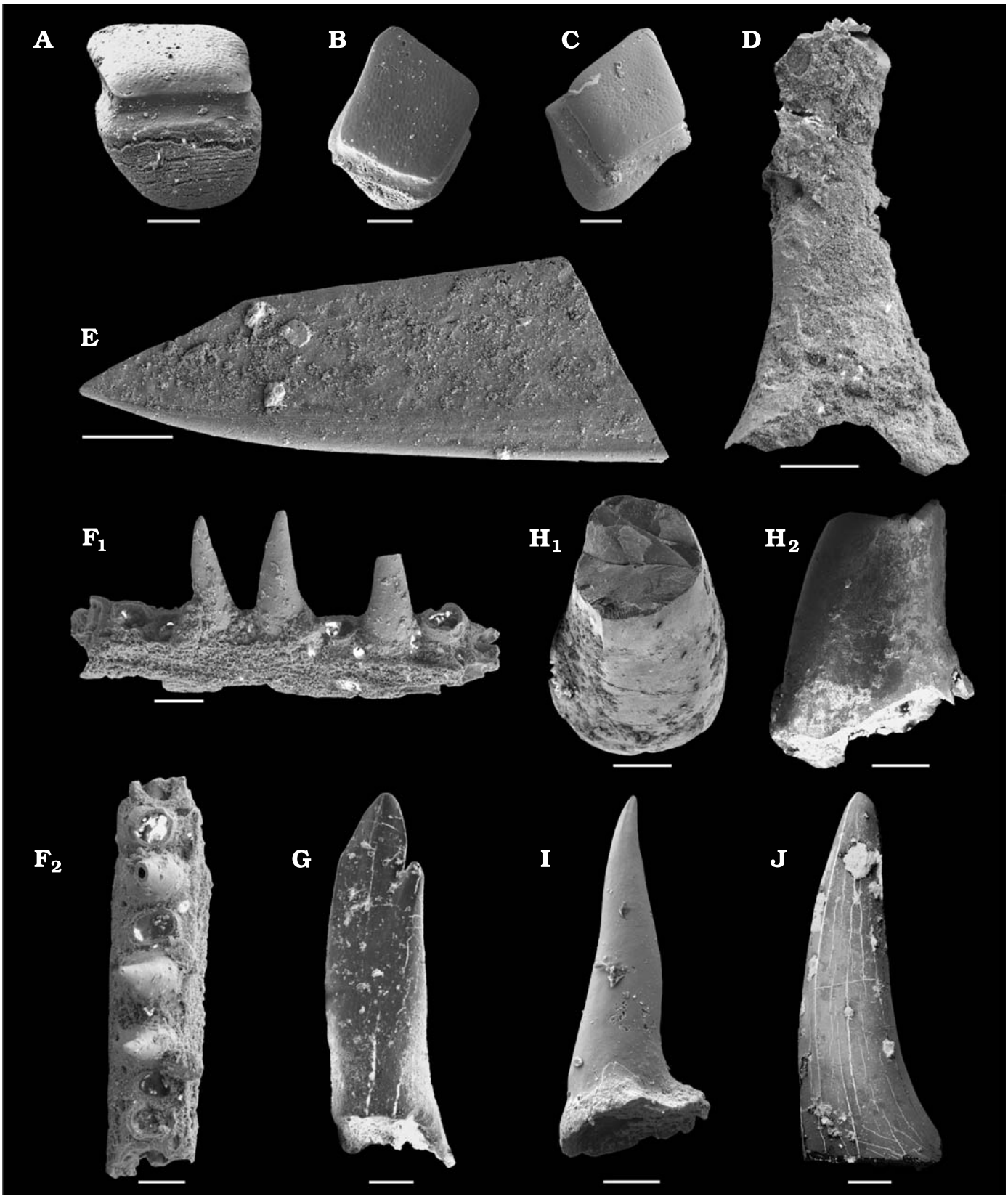

Fig. 8. Isolated vertebrate remains from Guardia Pisano. *Acanthodes* sp., Gzhelian–Asselian of Guardia Pisano, Sardinia, Italy. **A**. Scale FG 589/A/001, lateral view. **B**. Scale FG 589/A/002, dorsal view. **C**. Scale FG 589/A/003, dorsal view. **D.** Scapulocoracoid FG 589/A/007, lateral view. **E**. Spine fragment FG 589/A/008, lateral view. **F**. Branchiosaur jaw fragment FG 589/B/001, lateral (F_1) and occlusal (F_2) views. **G**. Bicuspid amphibian tooth FG 589/001 lateral view. **H**. *Orthacanthus*-like tooth fragment FG 589/O/001, oblique occlusal (H_1) and lateral (H_2) views. **I**. Lateral cusp of ?*Bohemiacanthus* sp. tooth FG 589/002, lateral view. **J**. Lateral cusp of *Xenacanthus* sp. tooth FG 589/O/003, lateral view. Scale bars: A–C, F, G, I, 100 μm, D–E, J, 300 μm, H, 500 μm.

The dimension of the Guardia Pisano lake is unclear but the limited size of the small intramontane trough of the Guardia Pisano Basin indicates a lake of probably just a few tens to hundreds of square kilometres. The aquatic fauna associated with *Lissodus* consists of *Acanthodes* (Fig. 8A–E), branchiosaur-like amphibians (Fig. 8F, G), and one or two xenacanthid shark genera (*Xenacanthus*, ?*Bohemiacanthus*) (Fig. 8I, J) as well as a diplodoselachid shark, most possibly *Orthacanthus*-like (Fig. 8H). The size and the cross section of this fragment fit well with this large xenacanthids, but the typical serration is not preserved because of corrosion.

Besides the dominance of *Lissodus*, the fauna of Guardia Pisano is similar to the lacustrine assemblage from the Early Permian (late Asselian after Werneburg et al. 2007) Perdasdefogu Basin (Ogliastra) in SE Sardinia (Fig. 1), which is generally characterised by different xenacanthid sharks (*Xenacanthus*, *Bohemiacanthus*), *Acanthodes*, branchiosaurs and various palaeoniscoid fishes (Freytet et al. 2002; Schneider et al. 2003; Werneburg et al. 2007).

Compared with other European Late Carboniferous and Early Permian lakes (e.g., Schneider et al. 1982; Gebhardt 1986, 1988; Schneider and Zajíc 1994; Boy 1998; Boy and Schindler 2000) the Guardia Pisano lake appears exceptional with its *Lissodus*-dominated vertebrate assemblage. For example, in the late Stephanian C Ilmtal lake of the Thuringian Forest Basin, *Lissodus* is associated with *Sphenacanthus vicinalis*, *Orthacanthus carbonarius, Xenacanthus, Bohemiacanthus,* palaeoniscids, branchiosaurs, and the large temnospondyl amphibian *Onchiodon* (Schneider and Zajíc 1994; Werneburg and Schneider 2006). Generally, *Lissodus* is a subordinate component in Late Carboniferous and Early Permian non-marine fish faunas.

Autecology of *Lissodus sardiniensis* sp. nov.

The size of *L. sardiniensis* sp. nov. is not clearly determinable because no articulated remains are preserved. On the basis of the assumption that teeth size/body length relations are similar to those in articulated remains of related forms (Broom 1909; Brough 1935; Antunes et al. 1990), a length of 20–30 cm is predicted for the Sardinian species.

The teeth of *L. sardiniensis* sp. nov. are weakly heterodont with lower crowned teeth occuring laterally. Therefore, the mesials (morphotype I) and symphyseals (morphotype II) were most probably used for clutching and the laterals (morphotype III) for crushing prey. This characteristic dentition indicates a durophagous lifestyle (Duffin 1985; Gebhardt 1988; Hampe 1991, 1996) as characterised by Recent rather small sharks of bottom dwelling habitat (Cappetta 1987; Compagno 1990). It is generally assumed that benthic hard-shelled invertebrates such as gastropods, crustaceans, and bivalves were probably the preferred prey of *Lissodus*. However, nothing argues against *L. sardiniensis* sp. nov. capturing other soft prey lacking a shell, which is indicated by clutching or grabbing morphology of the mesial or symphyseal teeth. In the opinion of Boy (1998) and Boy and Schindler (2000) the occurrence of *L.* cf. *zideki* was not necessarily bound to the occurrence of hard shelly benthos, but might be based on taphonomic bias. Furthermore, the dermal denticles also support the assumption of a bottom-dwelling habitat. Reif (1981) and Cappetta (1987) correlate small placoid scales with hook- or thorn-like crowns together with typical slow swimming Recent sharks in habitats near or on the bottom. Scales similar to those described here as morphotype 2 occur in the Recent *Echinorhinus brucus* and *Squalus acanthias*, which live in near-ground habitats (Reif 1981, 1985; Hampe 1996).

Synecology of *Lissodus sardiniensis* sp. nov. in lake Guardia Pisano

In a hypothetical food chain for the lakes of the Permian Saar-Nahe Basin Boy and Schindler (2000: fig. 1) considered *Lissodus* as a small durophagous-omnivorous bottom dwelling fish in the third trophic level as a secondary consumer. In the case of the lake ecosystem of Guardia Pisano, a food chain with five trophic levels seems to be plausible so far (Fig. 9) based on indirect evidence derived from functional-morphological interpretations. The first trophic level with phytoplankton as primary producers is generally not preserved but assumed as a food base for higher trophic levels, sensu Boy (1998) and Kriwet et al. (2007). The second level with zooplankton and hard shelly benthos is documented by the rare and badly preserved ostracods and small gastropods. The third level is composed of the durophagous-omnivorous *Lissodus*, the nectonic planctivorous *Acanthodes* and the branchiosaur-like amphibians as secondary consumers. One or two different predatory xenacanthid sharks (*Xenacanthus*, ?*Bohemiacanthus*) form the fourth level as tertiary consumers. It is commonly assumed that diplodoselachid piscivorous sharks, such as *Orthacanthus*, were the top predators in Late Carboniferous and Permian lakes. In this case, *Orthacanthus*-like tooth fragments indicate a fourth consumer in the fifth level of that food chain. However, we have doubts concerning the role of *Orthacanthus* in this and other lake ecosystems, because remains of juveniles and subadults are generally missing in the lakes and the occurrence of skeletons of adults is mostly restricted to single bedding planes in the lake deposits (e.g., Lake Heimkirchen in the Saar-Nahe Basin, Buxières lake in the Aumance Basin of the French Massif Central; personal observations by JWS). Possibly, large diplodoselachid sharks such as *Orthacanthus* and *Orthacanthus* (*Lebachacanthus*) were river dwellers and appeared sporadically only in the lakes, most possibly during drought periods with low water

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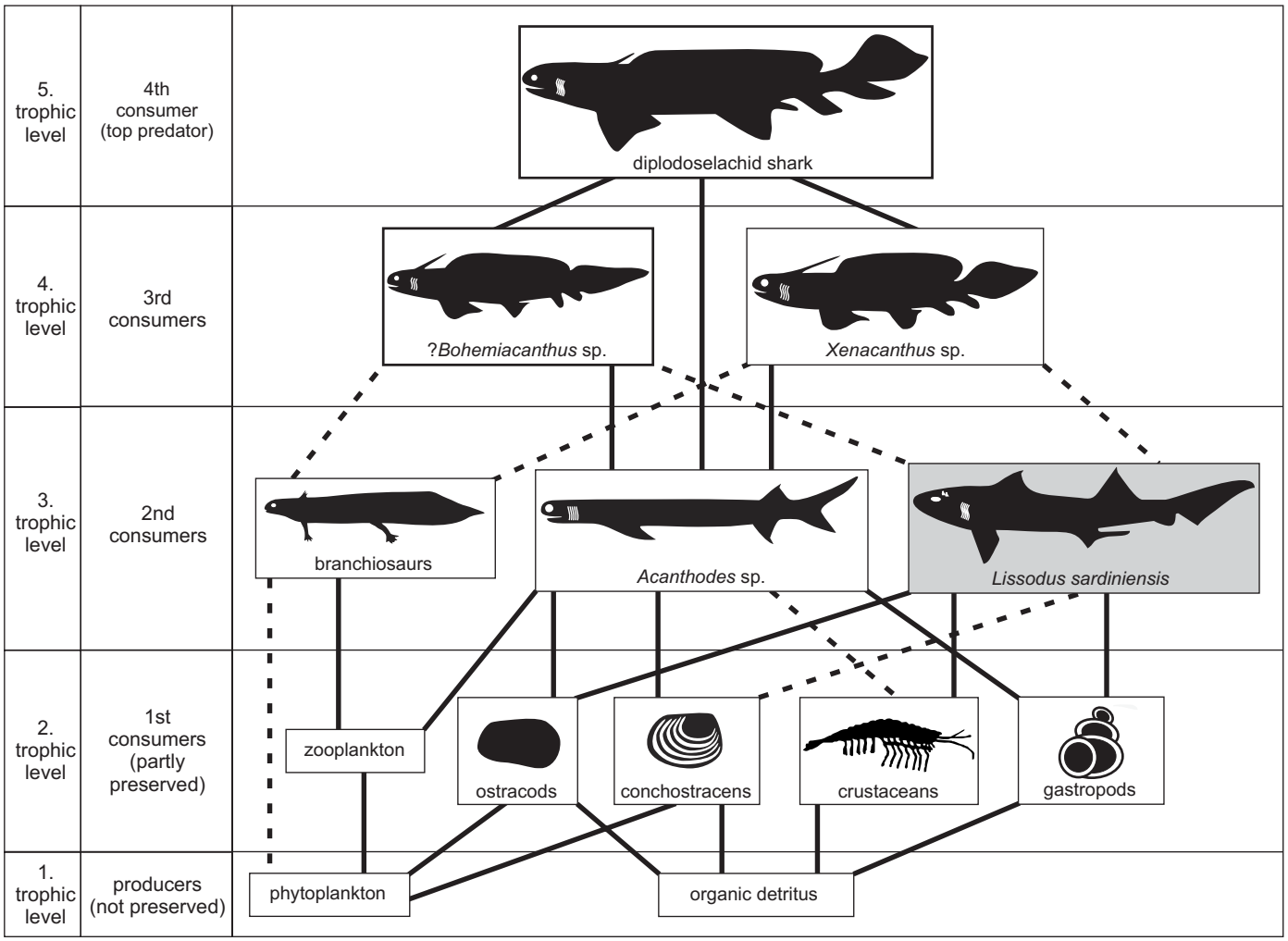

Fig. 9. Hypothetical food chain for the Early Permian Guardia Pisano lake environment based on indirect evidence (dashed lines) derived from functional-morphological interpretations (following Boy and Schindler 2000 and Kriwet et al. 2007). The producers are presupposed for the existence of the 1st (gastropods, ostracods) and 2nd consumers (undetermined branchiosaur, *Acanthodes* sp., and *Lissodus sardiniensis* sp. nov.), the 3rd consumer are xenacanthid sharks (*Xenacanthus* sp., ?*Bohemiacanthus* sp.), and a diplodoselachid-like shark forms the top predator.

levels in the rivers. This assumption is supported by the discovery of gastroliths of exotic rock pebbles in *Orthacanthus* (*Lebachacanthus*) skeletons. These pebbles were probably swallowed in the catchment area of the Early Permian Saar-Nahe river systems and are interpreted as ballast countering buoyancy (Boy 1994).

Palaeobiogeography of *Lissodus* in freshwater habitats

Lissodus is verified in nearshore marine deposits since the Late Devonian (Frasnian) (Trinajstic and George 2007) and for the remaining Late Palaeozoic (Johnson 1981; Tway and Zidek 1983; Duffin 1985; Derycke et al. 1995; Ivanov 1996, 1999, 2000, 2005; Lebedev 1996; Ginter 2002; Duncan 2004; Fischer 2008). From the current state of knowledge the first doubtless occurrence in non-marine deposits is from the Late Carboniferous (Stephanian B/C after *Pseudestheria* cf. *limbata,* Schneider et al. 2005a) of the Donetsk Basin, Ukraine (JWS, fieldwork 2002) (Fig. 10). Nevertheless, shark egg capsules of xenacanthids, i.e., *Fayolia*, and of hybodonts, i.e., *Palaeoxyris*, are known from true freshwater habitats (river deposits) at least since the Late Viséan early molasse deposits of the Variscan orogen in Germany (Rössler and Schneider 1997; Schneider et al. 2005b). Highly frequent glacio-eustatic and tectonically induced transgressions and regressions in the time frame from the Viséan to the Westphalian (Moscovian) form the background (comparable to the "estuary effect" by Park and Gierlowski-Kordesch 2007) for the colonisation of brackish and freshwater environments by initially marine fishes, and most probably by *Lissodus* too (Schneider and Reichel 1989; Rössler and Schneider 1997). Since the Late Stephanian (Gzhelian–Asselian) different species (*L. lacustris*, *L. lopezae*, and *L. sardiniensis* sp. nov.) form part of a highly diverse freshwater shark-association (*Orthacanthus–Xenacanthus–Bohemiacanthus–Sphenacanthus–Lissodus*,

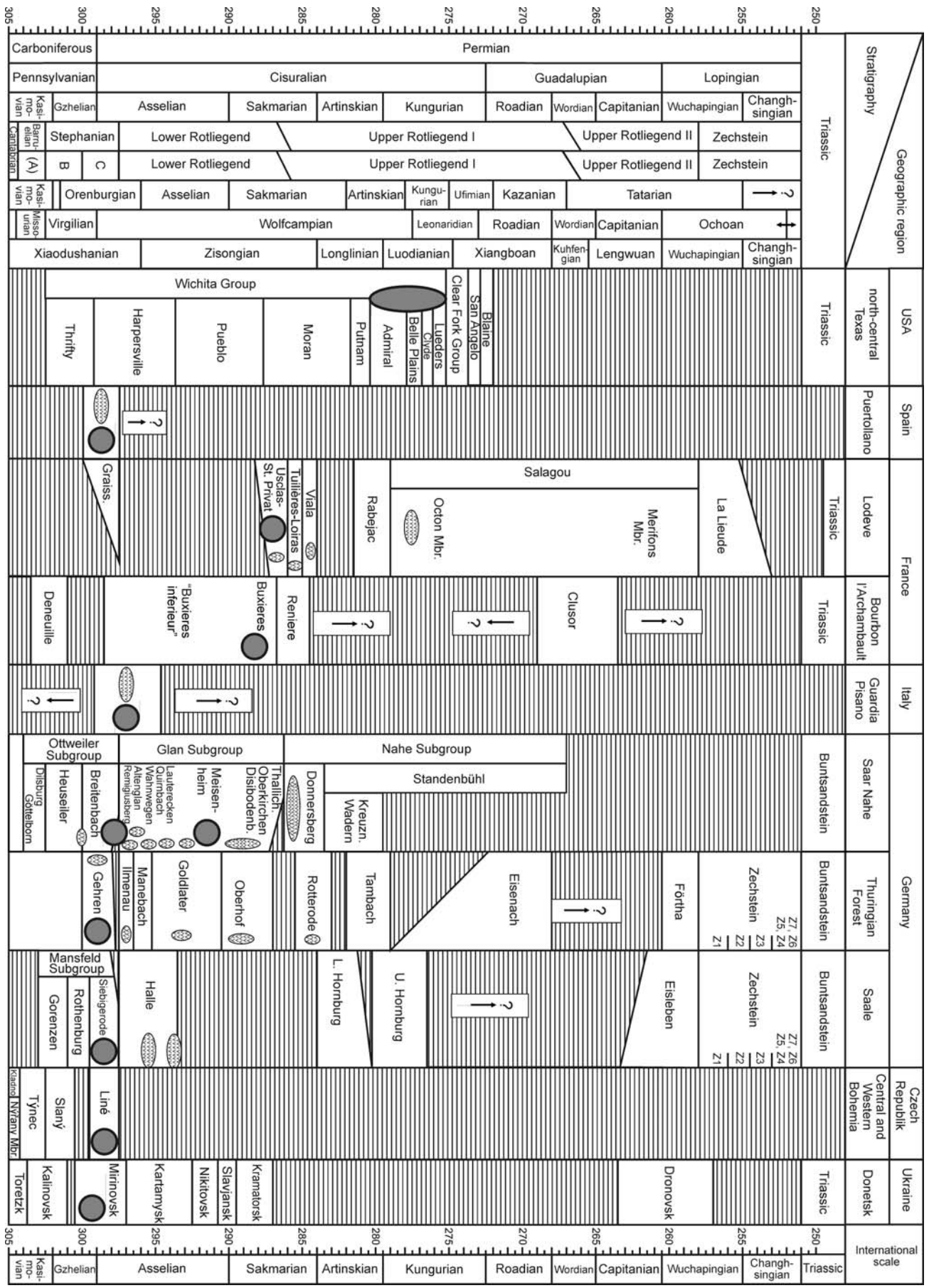

Fig. 10. Correlation chart of some late Pennsylvanian and Permian continental basins of Europe and marine-influenced Texas, USA. Grey circles indicate the occurrence of *Lissodus* remains (stratigraphy after Colmenero et al. 2002, Roscher and Schneider 2005, and Lucas 2006).

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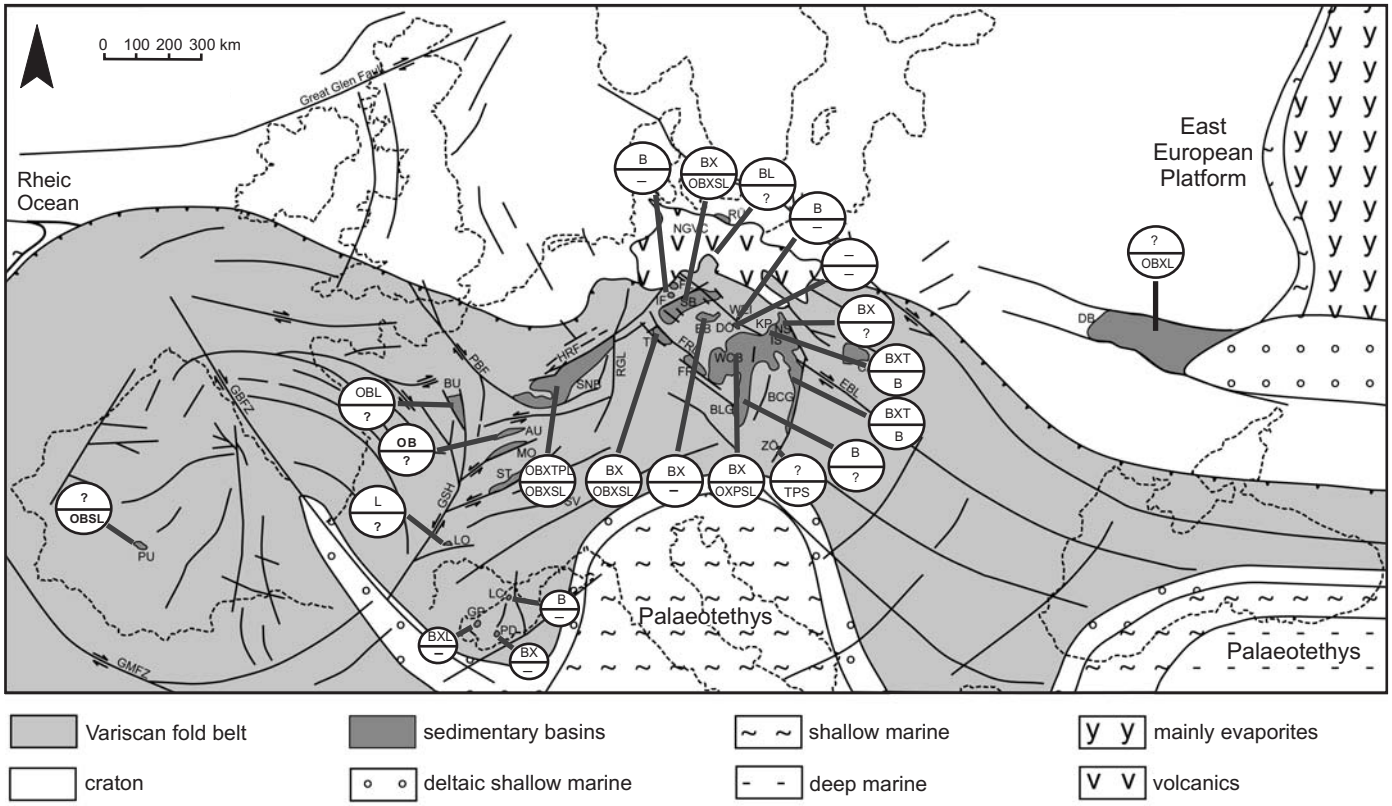

Fig. 11. Palaeobiogeography of hybodonts, ctenacanths, and xenacanthids from the Lower Rotliegend, Stephanian C (Late Carboniferous and Early Permian) based on current knowledge: B, *Bohemiacanthus*; L, *Lissodus*; O, *Orthacanthus*; P, *Plicatodus*; S, *Sphenacanthus*; T, *Triodus*; X, *Xenacanthus*; below the horizontal line – occurrences during Stephanian C (late Gzhelian–early Asselian), and above the horizontal line—occurrences during Lower Rotliegend (middle Asselian–early Sakmarian) (after Fischer 2005, new arranged after Schneider and Zajíc 1994). Palaeogeographic position of important Permo-Carboniferous basins (after Fischer 2005 and Roscher and Schneider 2006), the Late Permian Northern and Southern Permian Basin are omitted: AU, Autun Basin; BLG, Blanice Graben; BCG, Boskovice Graben; BU, Bourbon l'Archambault Basin; CA, Carpathian Basin; CR, Carnic Alps; DB, Donetsk Basin; DÖ, Döhlen Basin; EB, Erzgebirge Basin; EBL, Elbe Lineament; FL, Flechting Block; FRL, Franconian Lineament; FR, Franconian Basin; GBFZ, Golf of Biscay Fracture Zone; GMFZ, Gibraltar Minas Fracture Zone; GP, Guardia Pisano Basin; GSH, Grand Sillon Houllier Fracture Zone; HRF, Hunsrück Fracture; IF, Ilfeld Basin; IS, Intra Sudetic Basin; KP, Krkonoše Piedmont Basin; LC, Lu Caparoni Basin; LO, Lodève Basin; MO, Montceau les Mines Basin; NGVC, North German Volcanite Complex; NS, North Sudetic Basin; PBF, Pays de Bray Fracture; PD, Perdasdefogu Basin; PU, Puertollano Basin; RGL, Rhein Graben Lineament; RÜ, Rügen; SB, Saale Basin; SNB, Saar-Nahe Basin; ST, St. Etienne Basin; SV, Salvan-Dorénaz Basin; TF, Thuringian Forest Basin; TTFZ, Tornquist-Teysseyre Fracture Zone; WCB, Western and Central Bohemian Basins; WEI, Weissig Basin; ZÖ, Zöbingen.

Schneider and Zajíc 1994; Schneider et al. 2000) in the non-marine inter- and perimontane basins of Europe (Figs. 10, 11). In North America the first occurrence of *Lissodus* is reported from the Early Permian (late Artinskian– Kungurian) with *L. zideki* (Johnson 1981; Zidek et al. 2004) (Fig. 10).

It should be borne in mind that the tiny teeth of *Lissodus* from non-marine environments have been and will be overlooked in black shales, the main type of lacustrine sediment lithology investigated. In Europe, *Lissodus* became increasingly well known following the acid preparation of lacustrine limestones for ichthyolits by Gebhardt (1986, 1988). Further discoveries could easily change these following first tentative palaeogeographic interpretations.

As far as is known, *L. lacustris* is the commonest species group of this genus with the widest distribution in Stephanian C (Gzhelian–Asselian) (Fischer and Schneider 2007, 2008; Fischer 2008) from the Donetsk Basin (*L.* cf. *lacustris*), across the central- and western Bohemian basins of the Czech Republic (*L.* cf. *lacustris*; Zajíc 2000), the Saale and Thuringian Forest basins in eastern Germany (*L. lacustris* Gebhardt, 1988), to the Saar-Nahe Basin in western Germany (*L. lacustris*; Hampe 1991; Krätschmer 2005) (see Figs. 11, 12A). All these basins were connected during the Stephanian by a complex drainage system following different fracture zones (Schneider and Zajíc 1994; Schneider et al. 2000) allowing interbasinal migrations. The Central European Variscan orogen was levelled to low mountain ranges by at least the beginning of the Stephanian B (Roscher and Schneider 2006). Thus, the Variscan belt was not an insurmountable migration barrier to aquatic organisms between the northern and southern flanks of the Variscides (Werneburg et al. 2007). A connection between the Saar-Nahe Basin to the eastern Thuringian Forest and Saale basins is here assumed alongside the north-eastern runoff direction of the Saar Basin or along the northern part of the Hunsrück southern border fault zone. A connection to the Bohemian basins

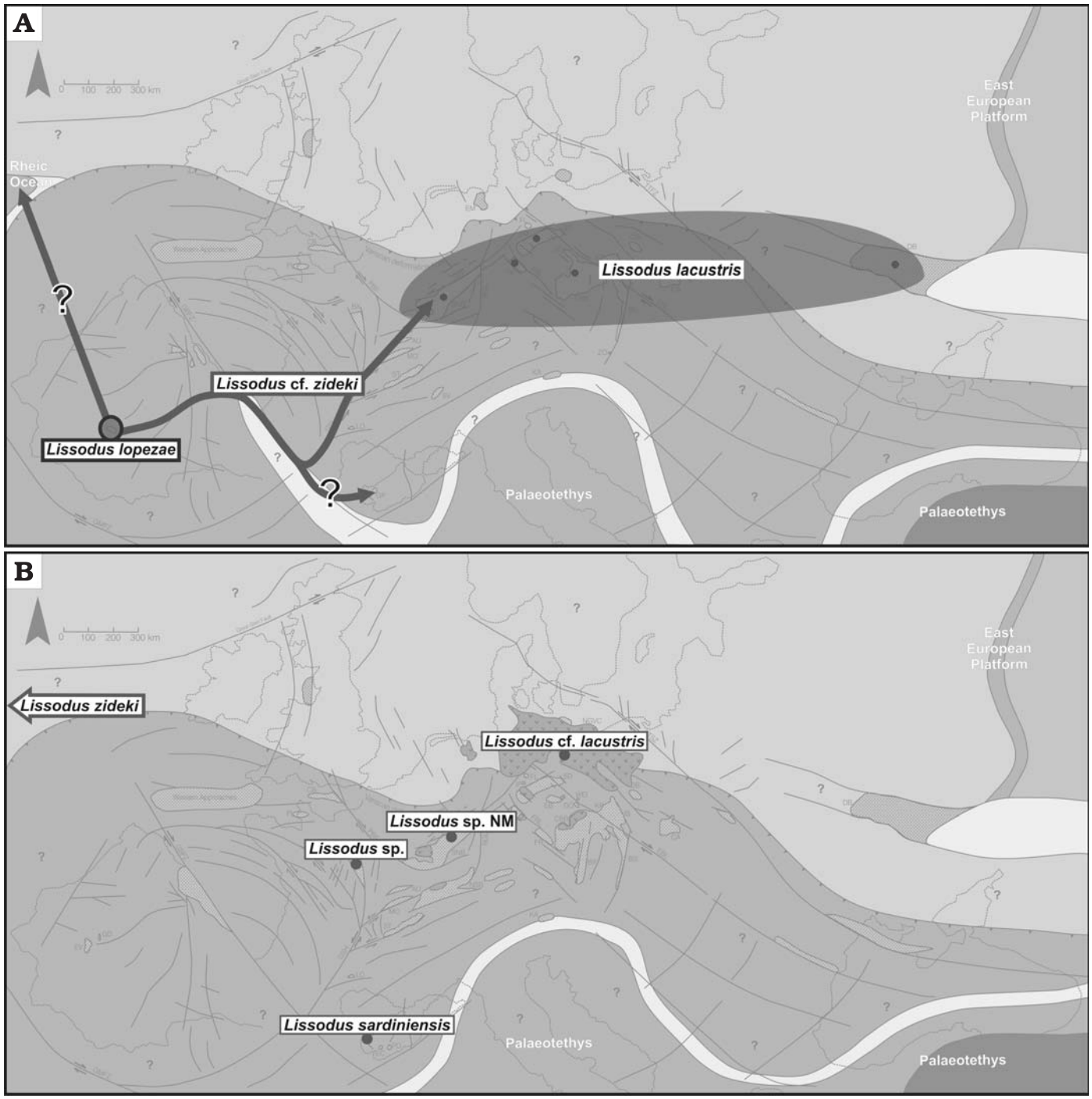

Fig. 12. Distribution areas of different *Lissodus* species in Europe. **A**. Latest Carboniferous/earliest Permian (Stephanian C): *Lissodus lacustris* is the most common species; *Lissodus lopezae* is restricted to Central Spain, and *Lissodus* cf. *zideki* shows a migration into the eastern Saar-Nahe Basin documenting the existence of migration possibilities between the single basins, other routes to the northwestern Rheic Ocean and to the southern Sardinia are just assumed. **B**. Early Permian (Asselian%Sakmarian): *Lissodus* cf. *lacustris* is a relic of *Lissodus lacustris*; *Lissodus* sp. (NM), *Lissodus* sp., and *Lissodus sardiniensis* sp. nov. are considered to be endemic relicts of *L.* cf. *zideki* in its former occurrence area; and the appearance of *L. zideki* in the late Early Permian of North America is also regarded as the result of NW migration.

might have followed the NW-SE striking Elbe lineament. Unfortunately, the only occurrence of Upper Carboniferous sediments in this area of the Döhlen Basin gives no hint of an extended river system (Schneider 1994). Therefore, a faunal exchange along the NW-SE striking Franconian lineament is much more plausible than along the Elbe Zone. Connection of the eastern Donetsk Basin to the Middle European basins is still unclear, but can be assumed by the occurrence of a typical Euramerian freshwater shark association (Schneider and Zajíc 1994).

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The Puertollano Basin in central Spain yielded two different species of *Lissodus* and one further record not designated to species level (Schneider et al. 2000; Soler-Gijón and Moratalla 2001). *L. lopezae* Soler-Gijón, 1997 was probably a rare, endemic species whereas *L.* cf. *zideki* (Soler-Gijón 1993) was much more common. We can assume that the latter migrated at the end of Stephanian C into the eastern Saar-Nahe Basin and there replaced the local *L. lacustris* (Boy and Schindler 2000) (Fig. 12A). If this was so, this migration probably took place from Spain using river systems linked to transform faults of the NW-SE striking Bay of Biscay Fracture Zone and toward to the N-S striking French Grand Sillon Houllier Fracture Zone in the south. Within this fault system, the migration into the eastern-situated Saar-Nahe Basin was possible. This is in concordance with Boy and Schindler (2000) who assumed a faunal immigration into the Saar-Nahe Basin from the west across France. Additionally, *L.* cf. *zideki* might be the ancestor of the North American *L. zideki* (Johnson 1981; Zidek et al. 2004), which first emerged in the late Early Permian (Artinskian-Kungurian) of Texas, Oklahoma and Nebraska. There, migration might have occurred alongside the Bay of Biscay Fault Zone northwards to the Rheic Ocean, which formed an embayment from the Panthalassa Ocean to mid-European areas until final closure during the Middle Permian according to a new palaeogeographic model by Kroner in Schneider et al. (2006) and Roscher and Schneider (2006). Generally, the fault and river systems linked to the marine realm could act as migration routes from the sea via rivers into the continental basins, likewise euryhaline fishes could migrate between different drainage systems via the sea. This does not stringently require marine influences on intracontinental basins as claimed by Schultze (2009).

The picture from the Lower Rotliegend (middle Asselian–early Sakmarian) differs from the Stephanian (Fischer and Schneider 2007, 2008). There are only local spots with possible endemic species of *Lissodus* in more or less restricted areas (Fig. 12B). *L. sardiniensis* sp. nov. might represent a descendant of the Spanish *Lissodus* species because of the resemblance of the teeth of *L. sardiniensis* sp. nov. with *L. lopezae* and *L.* cf. *zideki*, as described above. The former connection of Sardinia to Middle and Western Europe was most likely via the Bay of Biscay and Grand Sillon Houllier fault zones with no insurmountable migration barriers. *L.* cf. *lacustris* from the Early Permian (Asselian) of the Grüneberg Basin in the northeast German Brandenburg depression (Gaitzsch 1995) seems to be an endemic relict of the stratigraphic older form *L. lacustris*. Moreover, *L.* sp. (NM) from the Saar-Nahe Basin shows particularly strong affinities to *L. zideki* (Hampe 1996). Currently undetermined teeth and spines of *Lissodus*, which show some affinity with *L.* cf. *zideki*, are known from the middle Sakmarian (i.e., upper Autunian) Buxières Formation of the Aumance Basin, French Massif Central (Steyer et al. 2000; Kaulfuß 2004). Spines with hook-like denticles of the same age were found in the Usclas-St Privat Formation in the Lodève Basin of southern France. All these spotty occurrences or "relicts" might indicate a cut off of migration routes following the destruction of interbasinal river connections by Franconian tectonic movements around the Stephanian C/Lower Rotliegend boundary (Gzhelian–Asselian) at 302–297 Ma followed by a strong decrease in the diversity of freshwater sharks in most European basins (Fig. 11; Schneider and Zajíc 1994; Schneider et al. 1995, 2000) and possibly endemic evolution in the former trans-European (?–Euramerian) distribution area (Schneider 1989; Schneider et al. 2000). The increasing rarity and subsequent disappearance of *Lissodus* in the European basins is part of a step-wise extinction of the Carboniferous-type fish faunas of the palaeotropics during the Early Permian (Cisuralian). This step-wise extinction was caused by the interference of climatic and orographic physio-geographic processes. The general aridisation trend during the Permian shows a large scale change between dry and wet phases with a cyclic 7 to 9 Ma frequency (Roscher and Schneider 2006). Each subsequent wet phase is dryer than the foregoing wet phase. These, together with the increasing peneplanation of the Variscan orogeny as well as short-term but intense volcano-tectonics, increasingly prevented the development and existence of large permanent river systems. Increasing seasonal climate with augmented seasonal water discharge of rivers is indicated by extended braided river facies in the outspreading red beds during the European Early Cisuralian (Schneider and Gebhardt 1993; Schneider et al. 2006; Roscher and Schneider 2006). Extended large lakes appear in each wet phase but they are increasingly impoverished in their fish faunas. The LOD of *Lissodus* and *Orthacanthus* in the European basins falls into the fourth wet phase of Roscher and Schneider (2006), to which the Buxières and the Usclas-St Privat lakes belong. *Acanthodes*, which is often associated with *Lissodus*, has its LOD in the following fifth wet phase. The fourth wet phase marked the last occurrence of perennial lakes of the black shale facies in the disappearing palaeotropics, the biomes 1 to 3 of Ziegler (1990). In subsequent wet phases they are substituted by playa and sabkha lakes of semiarid and arid environments in the equatorial belt between 33°N and 33°S. Of course, freshwater sharks would not normally exist in temporary playa lakes. One interesting question remains unanswered so far—are there refuges for freshwater-adapted sharks such as *Lissodus* outside the equatorial arid belt in the areas of biomes 4 to 6 northerly and southerly of 33° latitude (compare with Roscher et al. 2008) in the Permian? Otherwise, the above discussed LOD of the Euramerian Palaeozoic freshwater species of *Lissodus* is the real LAD of these forms.

Conclusions

Numerous disarticulated remains of *Lissodus* from the lacustrine limestone of the Guardia Pisano Basin represent the first evidence of late Palaeozoic hybodont freshwater sharks from Sardinia, Italy. Furthermore, this is the southernmost occur-

rence of *Lissodus* yet known in the Late Palaeozoic of Europe. The number of specimens from this locality is exceptionally high in comparison to most other Palaeozoic localities with *Lissodus* remains.

The diagnostic feature of the newly erected species *L. sardiniensis* sp. nov. is a prominent cusp, flanked in all teeth by one pair of lateral cusps, which are bent in the direction of the larger central cusp. Three tooth morphotypes are recognisable, indicating weak heterodonty. In addition, fin spine fragments show a typical hybodontiform cross section, characteristic hybodont ornamentation, and a marginal alternating denticle row on the median posterior face. Moreover, three morphotypes are distinguishable within the scale assemblage. Teeth and scales suggest *L. sardiniensis* sp. nov. was probably a durophagous bottom-dwelling shark of 20–30 cm length. This is in concordance with palaeoecological assumptions concerning other species of *Lissodus* from freshwater environments. In a trophic chain of the Guardia Pisano lake ecosystem it adopted the role as secondary consumer on the third trophic level, together with the planctivorous *Acanthodes*.

Similarities with Carboniferous remains in Puertollano (Central Spain) and the Saar-Nahe, Thurinigan Forest, and Saale basins (all Germany) point to a complex drainage system connecting the European basins along different fracture zones during late Pennsylvanian times. This is also supported by the occurrence of *Lissodus* as a part of a uniform, widespread, and highly diverse shark-fauna association within the freshwater environments during the latest Carboniferous. After the volcano-tectonic events close to the Stephanian C/Lower Rotliegend (earliest Asselian) boundary, the destruction of the former stable drainage systems resulted in a noticeable depletion of shark faunas within most of the European Rotliegend basins. *L. sardiniensis* sp. nov. from Sardinia probably represents an endemic relict of the Stephanian distribution area of *Lissodus*, together with Early Permian finds from the French Massif Central and from the Saar-Nahe Basin.

The inference of the principle of actualism comparing fossil forms to extant ones must be handled with care. The view by Schultze and Soler-Gijón (2004) and Schultze (2009) considering Palaeozoic sharks from non-marine deposits as euryhaline forms which "moved into estuarine and lagoonal areas for spawning as extant anadromous forms" is not well supported, and it is also not in accordance with the critical discussion of actualistic conclusions on extinct forms by Schultze (2009). Such a regular migrations between marine and freshwater environments would implicate that a part of the life cycle was restricted to the sea. Instead of that it has been shown that some of the Late Palaeozoic hybodonts and xenacanthids completed their life cycles from the egg capsules to the adults in freshwater habitats. Although, a diadromous to anadromous lifestyle of the Guardia Pisano sharks cannot definitely be excluded so far it appears to be improbable. Therefore, *L. sardiniensis* sp. nov. is assumed to be fully freshwater-adapted.

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