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FIRST RECORD OF THE RARE MARINE REPTILE *THOLODUS SCHMIDI* FROM THE MIDDLE TRIASSIC OF THE SOUTHERN ALPS

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Abstract. *Tholodus schmidi*, a rare marine reptile of debated affinity and with a peculiar durophagous dentition, is for the first time recorded outside the Muschelkalk Basin of Central Europe. Parts of a mandibular ramus and a maxilla, both bearing teeth and nearly uncrushed, have been found in the upper Anisian (Balatonicus Subzone) of northeastern Italy. The tooth implantation is relatively complex, with both "alveolate" and "ankylosed" teeth. Disarticulated postcranial bones of an ichthyosaur have been found close to, but not in articular association with, the dentigerous bones of *Tholodus*. The humerus resembles that of immature individuals of the Chinese genus *Chaohusaurus*. This association, and some features of teeth and dentigerous bones, suggests that *Tholodus* might be a grippiid ichthyosaur.

Riassunto. *Tholodus schmidi*, un raro rettile marino di discussa affinità tassonomica e con una dentatura durofaga peculiare, è segnalato per la prima volta al di fuori del Bacino del Muschelkalk dell'Europa Centrale. È stato rinvenuto nell'Anisico superiore (Sottozona a Balatonicus) dell'Italia nordorientale ed è rappresentato da un ramo mandibolare incompleto e da un mascellare, entrambi dentigeri e poco compressi. L'impianto dei denti è relativamente complesso, con denti sia "alveolati" sia "anchilosati". Ossa postcraniali disarticolate appartenenti ad un ittiosauro sono state trovate vicino, ma non in connessione anatomica, alle ossa dentigere di *Tholodus*. L'omero assomiglia a quello degli individui immaturi del genere cinese *Chaohusaurus*. Questa associazione e alcuni caratteri dei denti e delle ossa dentigere, suggeriscono che *Tholodus* possa essere un ittiosauro grippide.

Introduction

Tholodus schmidi v. Meyer is a rare but peculiar marine reptile known from fragmentary remains from the Middle Triassic of Central Europe. It is characterized by large teeth, which are capped by dark, bulbous crowns with apicobasally wrinkled enamel, and marked by high "roots" with folded dentine (Sander & Mazin 1993). The fossil record of *Tholodus* is rather limited and consists of seven fragmentary

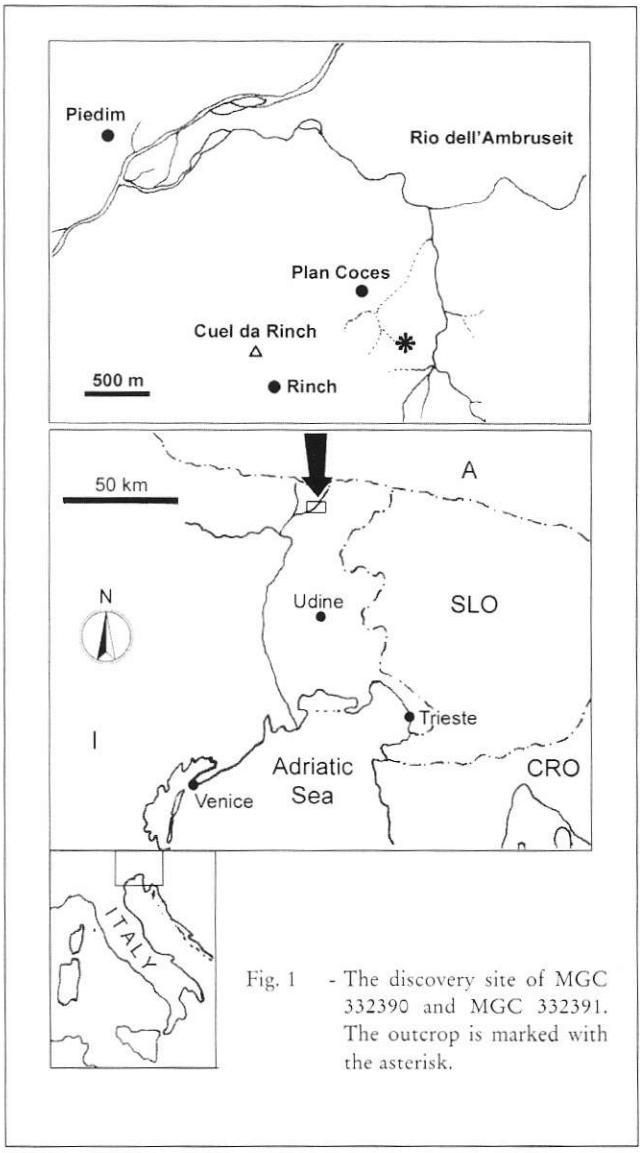

Fig. 1 - The discovery site of MGC 332390 and MGC 332391. The outcrop is marked with the asterisk.

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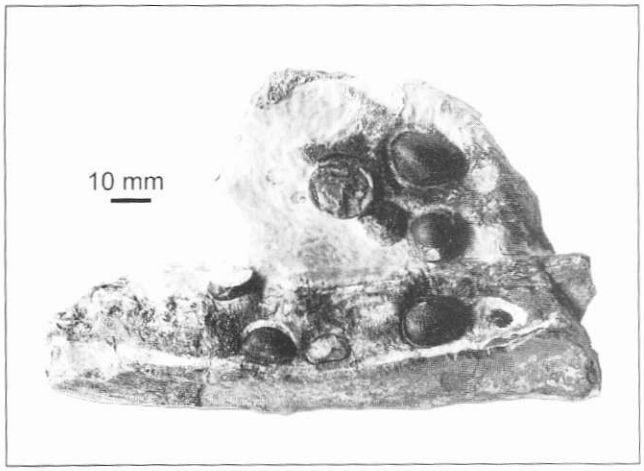

Fig. 2 - MGC 332390, *Tholodus schmidi*. The two dentigerous bones as preserved before complete preparation. Scale bar is 10 mm.

tooth-bearing bones and several isolated teeth from Germany (v. Meyer 1851; Fritsch 1906; Jaekel 1907; Peyer 1939; Sander & Mazin 1993; Hans Hagdorn, pers. comm.), and a partial lower jaw from Poland (Sander & Mazin 1993).

In 1996 Mr. Mario Campibelli donated two small blocks of rock with fossil bones to the Museo Geologico della Carnia of Ampezzo (Udine Province, NE Italy). The blocks were collected from a single outcrop near the small village of Plan Cocés (Piedim, Arta Terme Municipality, Udine Province; Fig. 1) and contain tooth-bearing bones referable to *Tholodus* and ichthyosaurian bones, respectively. The two specimens are described here.

Terminology

The terminology adopted for features of the ichthyosaur humerus is that of Motani (1999a), and that concerning dentition is from Peyer (1968), Edmund (1969) and, as far as it is possible, from Motani (1997b). In accordance with Peyer (1968), I use "base" instead of "root". As for the taxonomy of ichthyosaurs, I refer to Motani (1999b) and Maisch & Matzke (2000).

Acronyms: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; MFSN, Museo Friulano di Storia Naturale, Udine; MGC, Museo Geologico della Carnia, Ampezzo.

Systematic paleontology

Class **Reptilia** Linnaeus, 1758

Order **Ichthyosauria** Blainville, 1835

Family Grippiidae? Wiman, 1929 nom. transl. ex Grippidia

Genus *Tholodus* v. Meyer, 1851

Type species: *Tholodus schmidi* v. Meyer, 1851 (monotypical)

Tholodus schmidi v. Meyer, 1851

(Figs 2 to 8)

1851 *Tholodus Schmidi* Meyer H. v., pl. 31, figs. 25-28.
1906 *Tholodus Schmidi* - Fritsch, pls. IX-X.
1907 *Tholodus* - Jaekel, pp. 30, 32-33, figs. 14-17.
1932 *Tholodus schmidti* - Smith Woodward, p. 279.
1939 *Tholodus schmidi* - Peyer, figs. 1-21; pls. 1-2.
1969 *Tholodus schmidi* - Kuhn, p. 60.
1993 *Tholodus schmidi* - Sander & Mazin, p.146; fig. 1.
1997 *Tholodus* - Rieppel & Hagdorn, p. 139.
1997 *Tholodus* - Lucas, figs. 2-3, p. 429.
1998 *Tholodus schmidi* - Sander & Faber, p. 155.
1999 *Tholodus schmidi* - Hagdorn & Rieppel, p. 659, fig. 4.
2000 *Tholodus schmidti* - Sander, p. 14, fig. 3.

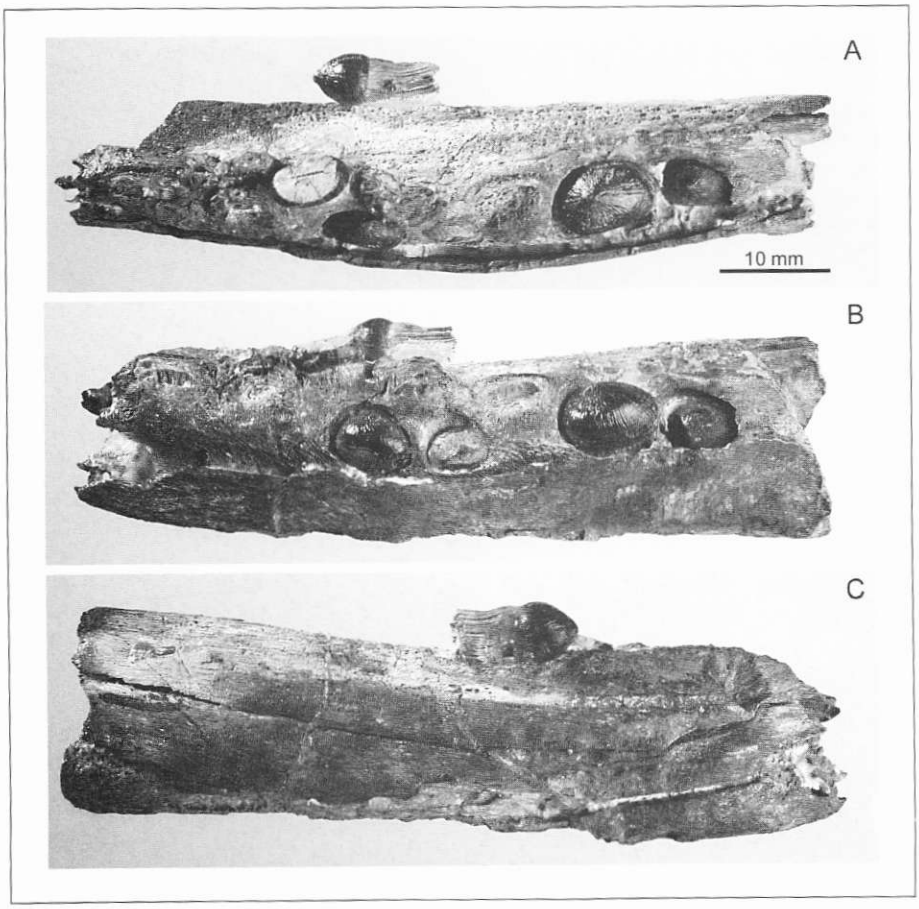

Fig. 3 - MGC 332390, *Tholodus schmidi*. Right lower jaw ramus: A, dorsal; B, medial; C, lateral. Scale bar is 10 mm.

Description

The tooth bearing elements were originally preserved on a single fragment of limestone (MGC 332390). They consist of a partial lower jaw ramus and a nearly complete dentigerous bone identified as a maxilla (see below). They were originally placed close to each other, with the long axes arranged in a V-shape (Fig. 2). An isolated tooth is preserved along the labial margin of the lower jaw ramus. The two specimens are incomplete because of fracturing and weathering of the bed containing them. The bones have been prepared from the limestone matrix mechanically and chemically (diluted formic acid buffered by calcium phosphate). They are preserved three-dimensionally and suffered only slight compression and deformation.

Mandible. The mandibular segment is a posterior portion of the right ramus, 140 mm long (Figs. 3-4). The lower jaw is slender, with all the bones very elongated anteroposteriorly. The specimen suffered a slight distortion in the vertical (sagittal) plane, such that the labial half is unnaturally higher than the lingual one, and the splenial is detached from its contact with the dentary (see Figs. 3B, 4B, and 5A).

The splenial makes up the lingual side of the mandibular fragment as well as, at least anteriorly, the ventral margin and the lower part of the labial side. The mid-posterior portion of the ventral part of the mandible is missing; thus the posteroventral extent of the splenial remains unknown. The bone is thin dorsally and becomes much thicker (wider) ventrally. The slightly deformed dentary constitutes the dorsal side and the upper part of the labial side of the mandibular segment. In labial view, it is a low and long bone, blade-like posteriorly and thick anteriorly. On the labial side, it wraps around the dorsal part of the surangular (Fig. 5A) and anteriorly it wraps around the upper part of the angular (Fig. 4C). A deep, wide groove runs longitudinally along this side, shallowing posteriorly. The lingual side was originally in contact with the splenial, but deformation displaced it, exposing the rough and spongy sutural surface. Teeth occur lingually on the dorsal side of the dentary, whereas the labial half of this side is a flat platform without teeth and with a finely spongy texture, which becomes wider anteriorly (Fig. 4A). The labially exposed surangular is wedge-shaped, tapering rostrally and becoming thin ventrally. It covers the dorsal part of the angular. A posterior fracture cutting across the jaw shows that a dorsal lamina of the angular fits inside a groove on the ventromedial part of the surangular (Fig. 5A).

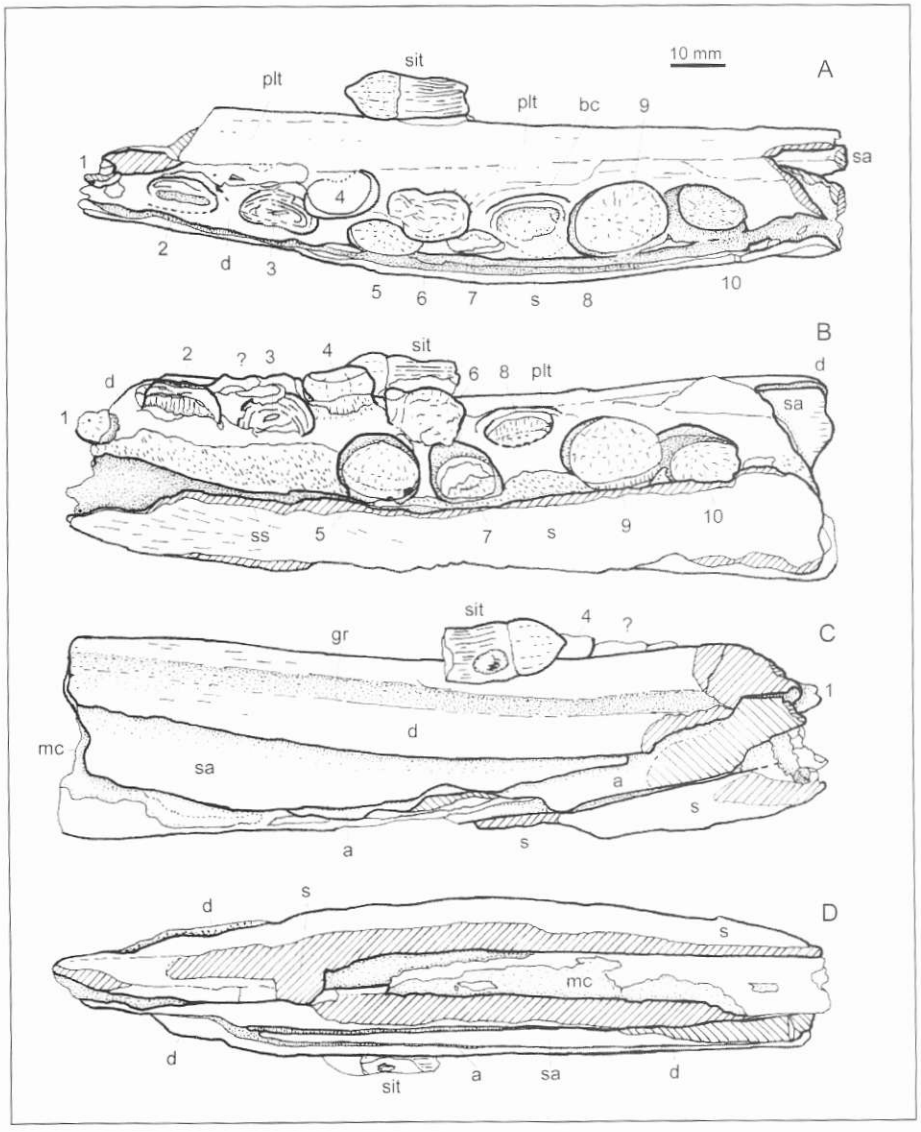

Fig. 4 - MGC 332390, *Tholodus schmidi*. Right lower jaw ramus, drawings. A, dorsal; B, medial; C, lateral; D, ventral. Cross-hatch pattern indicates the broken edge of the bone. Scale bar is 10 mm. Abbreviations: a, angular; bc, black layer of cementum or attachment bone; d, dentary; gr, groove; mc, Meckel channel; plt, labial platform of the dentary; s, splenial; sa, surangular; sit, single isolated tooth, probably a mesial mandibular one; ss, dentary sutural surface for the splenial; 1-9, teeth 1-9 (see text); ?, possible tooth remains.

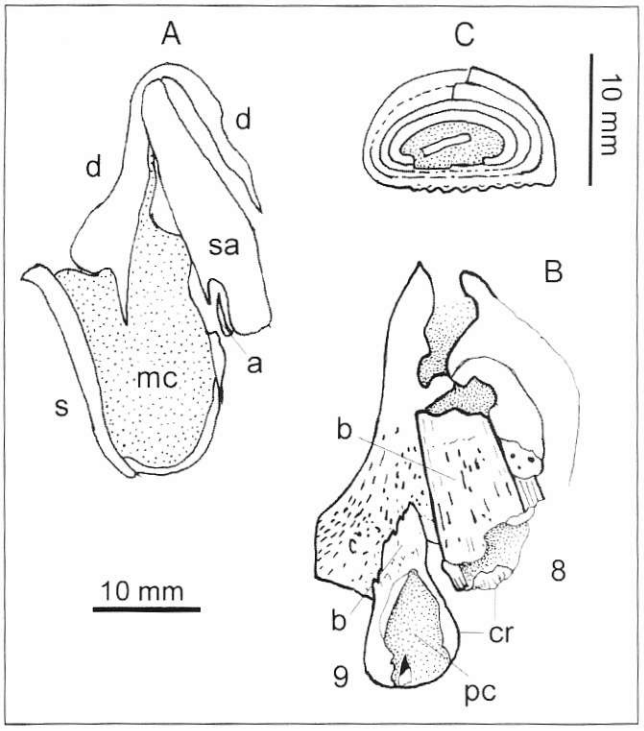

Fig. 5 - MGC 332390, *Tholodus schmidi*. Cross-sections of bones and teeth. A, Posterior cross-section of the lower jaw portion; B, Posterior cross-section of the maxilla (the dorsal side is the left side in the figure); C, diagonal (from upper labial to basal lingual) section of mandibular tooth 3. Abbreviations: a, angular (dorsal lamina); b, fluted base; cr, crown; d, dentary; mc, Meckel channel; pc, pulp cavity; s, splenial; sa, surangular; 8-9, teeth 8-9 (see text). Limestone matrix is stippled. Scale bar is 10 mm.

The bone exhibits a fine spongy texture on all of its non-sutural surfaces. Meckel's channel is filled with limestone.

Mandibular teeth. Ten tooth positions are present on the fragment. Teeth are arranged in a single row on the posterior and anterior parts of the lower jaw fragment, whereas in the mid-part the teeth are set in two rows. I numbered the teeth starting from the first anterior (tooth 1) to the last posterior (tooth 10). Of course, this numbering system does not correspond to the original count of tooth positions, as the mandible is incomplete. For convenience, I describe the teeth from rear of the bone, because they are better preserved.

The two rearmost teeth are set in large and relatively deep alveoli (Fig. 6A). The two alveoli are separated from each other by a very thin septum. The lingual wall of each alveolus is also extremely thin. This wall is lower than the labial wall, but this is at least partly a result of deformation of the dentary caused by compression. The posterior tooth (tooth 10) is not yet functional, as its crown does not rise from the alveolus. The crown of the other tooth (tooth 9) is also only partly elevated above the margin of the alveolus. The crown of the posterior tooth is at least 12.5 mm long mesiodistally and 9 mm wide labiolingually; that of the other tooth is 17.5 mm long, about 11.5 mm wide and about 10 mm high apicobasally. Therefore, the crowns of the two teeth are elliptical, longer than wide. Their superficial colour is bright black and they have a pointed apex. The ornamentation of the surface consists of wrinkle-like, irregular, but long, apicobasal ridges (Fig. 6B). Sometimes the ridge starts as a single wrinkle from the apex and bifurcates on the upper part of the crown. Thin transverse (equatorial) grooves mark growth stages of the crown, making a reticulate pattern with the wrinkles. The crown of tooth 9 is slightly asymmetrical, i.e., the pointed apex occurs more mesially than distally. The base of this tooth is gray coloured and finely fluted. The bases are not ankylosed to the wall of the alveolus, but it is not possible to discern whether they are ankylosed at the bottom. Tooth position 8 is represented by a shallow socket 11 mm long, 6 mm wide, and 4 mm deep on the labial side (Fig. 6C). The labial side of the socket is decidedly deeper than the lingual side, and this is not caused by deformation. The remains of the fluted tooth base are still preserved in the labial margin of the socket, ankylosed to the bone and penetrating some millimeters inside. A black layer, probably of cementum or dense attachment bone, occurs labially between the base and the mandibular bone. Thus, the tooth base has this kind of attachment only along the labial side of the socket, whereas along the lingual side it merely rests against the bone. Tooth 7 is represented by a relatively small, erupting elliptical crown, whose exposed part is 11 mm long mesiodistally. The tooth seems to be placed in a socket with a very thin lingual wall that is decidedly lower than the labial wall. The thin, black layer of enamel is missing in some places, showing the underlying lighter dentine. Tooth 6 is firmly ankylosed to the bone and is broken. The preserved lower part of the crown is approximately 15 mm long and does not show any trace of a pulp cavity or any other inner structure. The base is not exposed; thus it is either lacking or is fully enclosed inside the bone. Tooth 5 (Fig. 6D) is in the same condition as tooth 9, but is decidedly smaller (the crown is about 13.5 mm long). Features of the alveolus are the same as those of tooth 7, with a lingual wall decidedly lower than the labial wall. Tooth 4 is 13.5 long, 7.5 mm wide and 4 mm high. The upper part of the crown is completely worn away. It shows a wide elliptical wear-facet dorsally (Fig. 6E-F) and another smaller one labially. The latter appears to be a piece of crown split away during feeding. There is no pulp cavity or any other inner structure. The fluted base is ankylosed to the bone and is exposed only lingually, rising up to 4 mm above the bone surface. There is a distinct neck between crown and base, marked also by the different colour of the two parts. The portion of the dentary bearing teeth 1-3 is compressed and partly deformed. Only a cross-section of the tooth where it meets the bone surface is preserved for tooth 3. The plane of the section

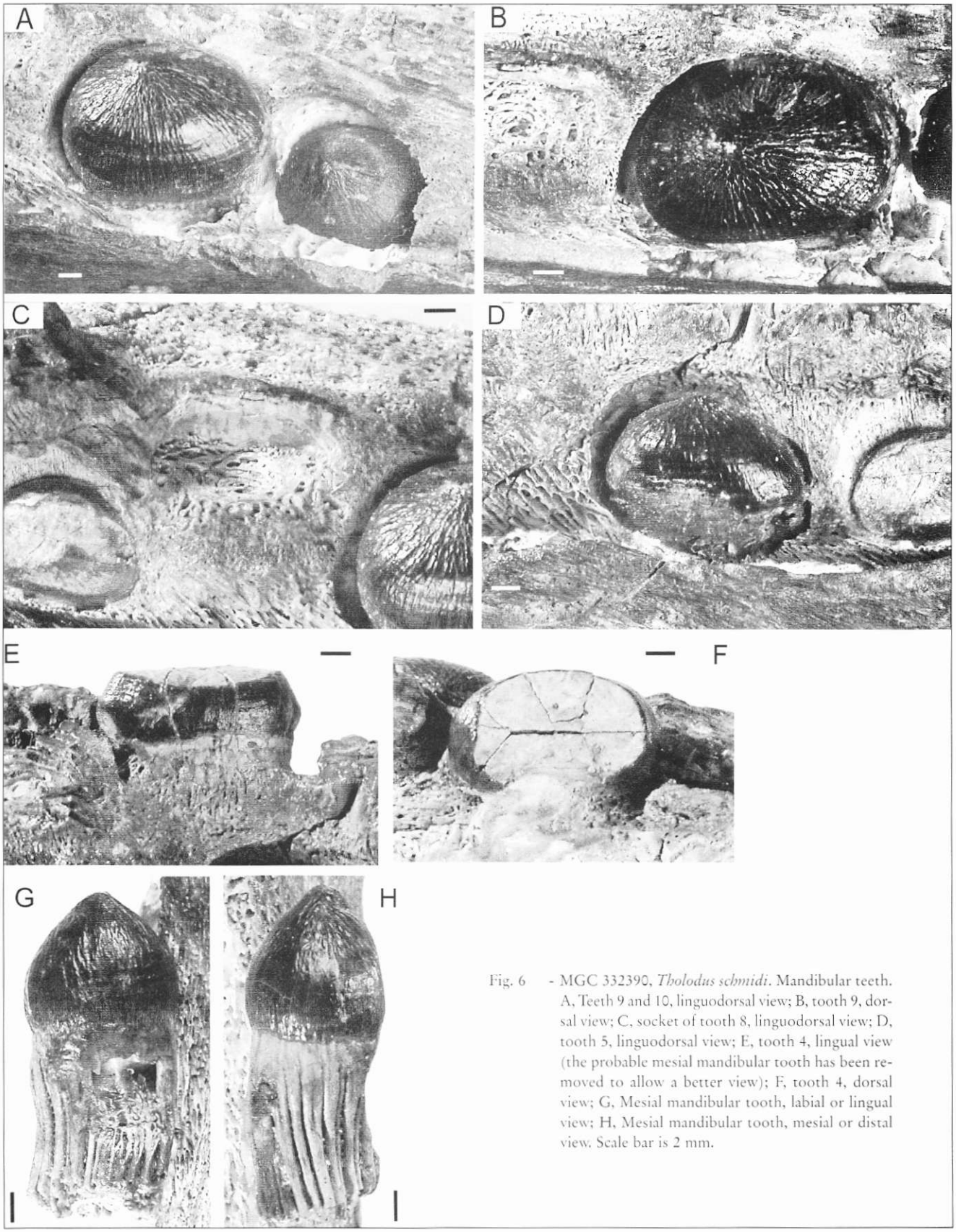

Fig. 6 - MGC 332390, *Tholodus schmidi*. Mandibular teeth. A, Teeth 9 and 10, linguodorsal view; B, tooth 9, dorsal view; C, socket of tooth 8, linguodorsal view; D, tooth 5, linguodorsal view; E, tooth 4, lingual view (the probable mesial mandibular tooth has been removed to allow a better view); F, tooth 4, dorsal view; G, Mesial mandibular tooth, labial or lingual view; H, Mesial mandibular tooth, mesial or distal view. Scale bar is 2 mm.

is inclined, intercepting the crown from the upper labial side to the lower lingual side. This section is elliptical, 14.2 mm long and about 9.5 mm wide, but with a flatter lingual margin and a more convex labial margin (Fig. 5C). The mesial, distal and labial margins of the section show 4 black layers of dentine, and there is a pulp cavity about 7 mm long mesiodistally (Fig. 5C). This inner layering resembles that of a *Tholodus* tooth cross-sectioned

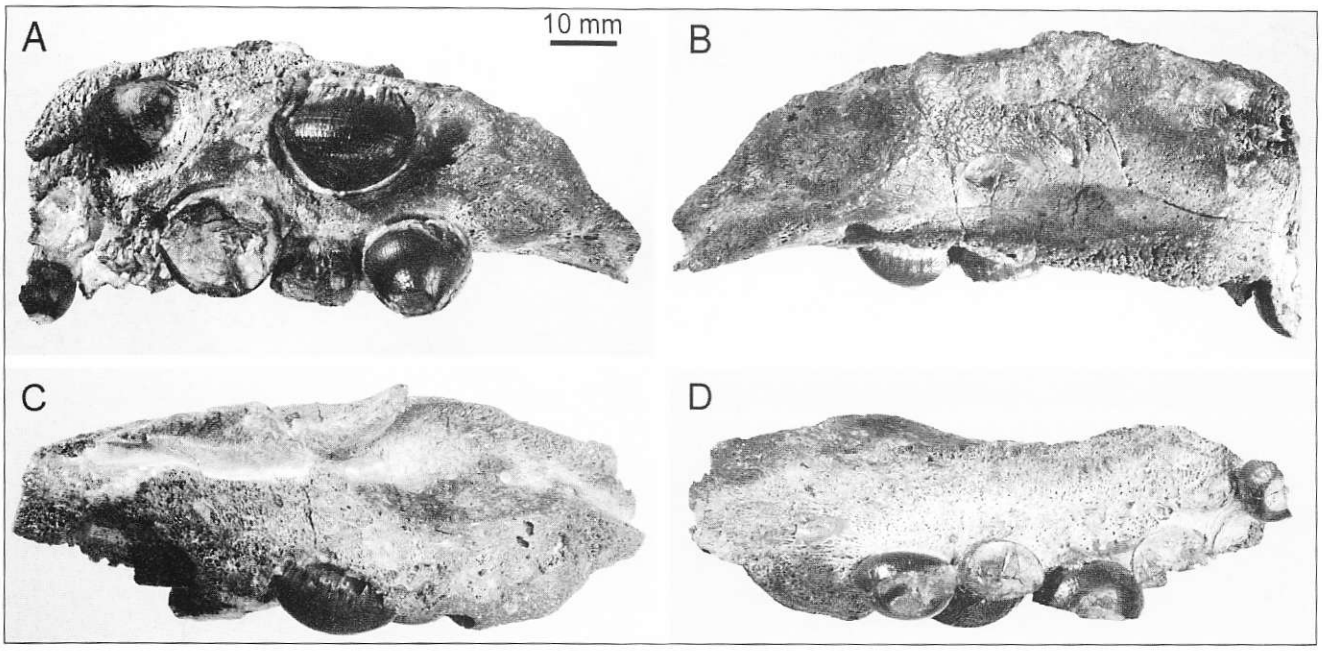

Fig. 7 - MGC 332390, *Tholodus schmidi*. Left maxilla. A, ventral; B, dorsal; C, lingual; D, labial.

at the upper part of the base (see Peyer 1939, fig. 6). The fluted base, visible lingually in cross section, appears to be fused to the bone. The remains of an old tooth, nearly completely worn away, are possibly present immediately labial to tooth 3. Tooth 2 is preserved similarly to tooth 8, with the labial side of the base set inside the bone. The socket is 15.4 mm long, and only about 5 mm wide due to labiolingual deformation. Tooth 1 is represented by only the apical portion of a crown with a small pointed apex, which indicates that the tooth was small. The surface shows the same ornamentation as tooth 10. The tooth is set in an alveolus.

A single isolated tooth is preserved on the dentary along the laterodorsal margin of the lower jaw (Figs. 3-4, 6G-H). The overall morphology of the tooth and the ornamentation of the crown surface is similar to that of the mandibular teeth described above, but the morphology of the crown is somewhat different. The crown is pagoda-shaped, with a mesiodistal oval cross-section, 10.4 mm long, 9 mm wide and 10 mm high. The apical part is pointed, and bears no traces of wear. The base is cylindrical with an elliptical cross-section (maximum length 11 mm, maximum width 6.7 mm) and 12 mm high. It is strongly fluted, due to deep infolding of the dentine. About 15 folds are present in side view; they are hollow tubules open at the side facing the internal part of the base, and the wider ones bifurcate approaching the crown. The internal part of the base is hollow, the folded dentine being like a fence. The tooth is removed from its natural seat in the bone. This suggests that its was not ankylosed to the bone or cemented at the base of the alveolus and its implantation was probably thecodont. There is a depression with an opening along one of the outer sides of the base, that allows a view of the hollow interior. This structure resembles a resorption facet, but is most probably an artifact of preparation. If actually a natural structure, it would suggest that a growing tooth contacted the functional one.

Maxilla. The other dentigerous bone (Figs. 7-8) is elongate (length 90 mm), narrow (maximum width, excluding the teeth, is 30 mm) and low (maximum height, excluding the teeth, is 31.2 mm). The tooth-bearing side is flat and platform-like (Figs. 7A, 8A). The opposite side is slightly concave (Figs. 7B, 8B). One of the ends of the bone is broken and exposes the element in cross-section (Fig. 5B). The other end is deeply notched and sends a process forward (Figs. 7B, 8B). Thus, that end bordered a wide cavity. The notch is well-exposed in one of the side views (Figs. 7C, 8C). In this side the surface of the bone is vertical and rough; i.e., it probably represents a sutural surface. The opposite outer side is also vertical and has two rough sutural surfaces (Figs. 7D, 8D). The notch continues with a channel or groove partly closed by the compressed overhanging dorsal flange (Figs. 7C, 8C). A very large neurovascular foramen connects the dorsal surface with the surface of the notch (Figs. 7B, 8B).

This bone resembles a *Tholodus* specimen tentatively identified as a left maxilla by Peyer (1939, figs. 1-2; pl. 2, fig. 1). Both are relatively low and elongated, they bear teeth arranged in two rows in some points, and have an anterior notch and a large foramen in a corresponding position. Assuming Peyer's identification is correct, and considering a symmetrical arrangement of teeth in the upper and lower jaws, the Italian specimen is a left maxilla.

The bone is incomplete posteriorly, whereas only a small fragment of the anterior process is missing and only

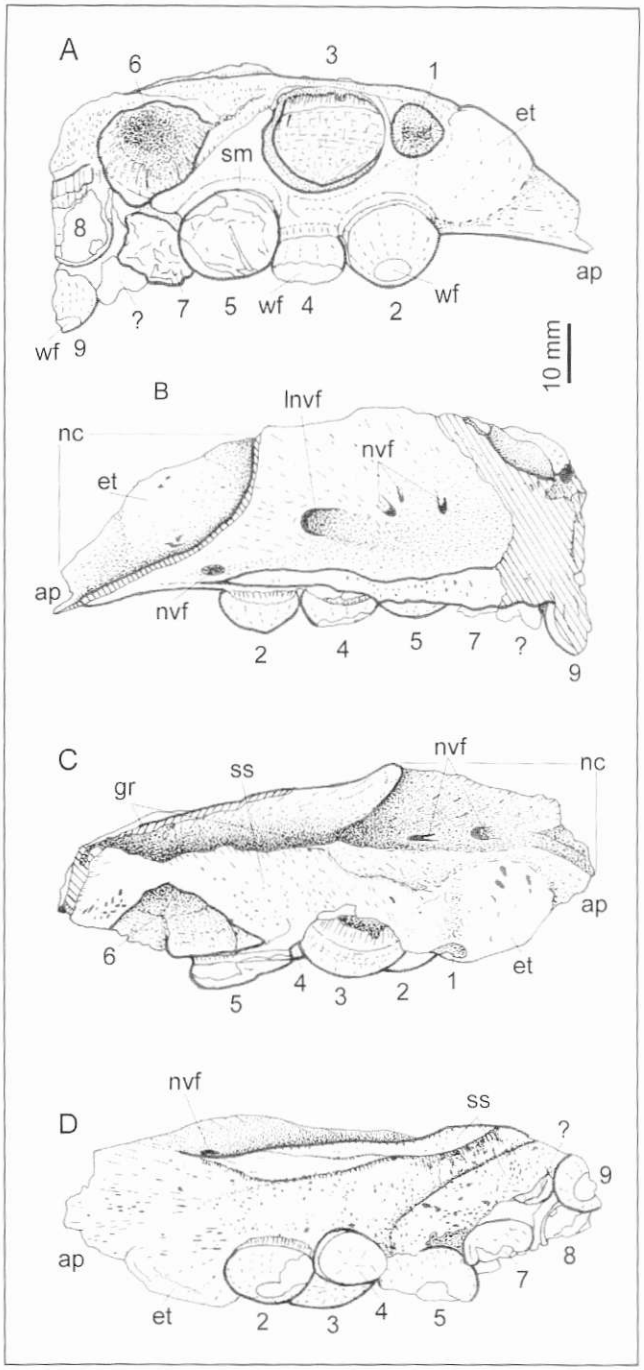

Fig. 8 - MGC 332390, *Tholodus schmidi*. Left maxilla, drawings. A, ventral; B, dorsal; C, lingual; D, labial. Cross-hatch pattern indicates the broken edge of the bone. Abbreviations: ap, anterior process; et, erupting tooth still completely inside the bone; gr, lingual groove; nc, notch; lnvf, large neurovascular foramen; nvf, neurovascular foramen; sm, smooth band of cementum or dense attachment bone; ss, sutural surface; wf, wear facet; 1-9, teeth 1-9 (see text); ?, possible remains of a nearly completely worn away tooth.

the dorsal portion of the rostral part had worn away. The other surfaces were embedded in limestone when I prepared the specimen, and so they have not been affected by fracture or recent weathering. A very large (its main axis is about 7 mm) neurovascular foramen piercing the dorsal surface enters the posterior end of the notch. The dorsal surface posterior to the foramen shows an anteroposteriorly elongated, relatively shallow and wide depression which gives the surface a concave aspect. Three smaller neurovascular foramina pierce this surface. A process slightly bent medially is sent anteriorly. This process borders the labial margin of the notch. A large neurovascular foramen opens labiodorsally in its proximal part. This foramen is probably related to a corresponding foramen in the notch surface. The ventroproximal part of the process is inflated because of the presence of a growing tooth still completely inside the bone (see below). The dorsal, thin "roof" of the notch is only partly preserved, because the anterior part was worn away. A narrow, deep and low groove runs along the lingual side, from the posterior end to the notch. The flange "roofing" this groove is compressed dorsoventrally, and consequently the groove has been partly closed. Three neurovascular foramina pierce the surface of the notch. The labial side of the maxilla has two bands of very rough bone which probably comprise a sutural contact with another bone. There are possibly two or three sutural facets. The lingual side also has a rough surface immediately ventral to the groove, suggesting that the bone was open and possibly sutured to another element along this side. The bone surface is always more or less spongy or cancellous. The cross section shows that the bone close to the dorsal surface is finely layered.

Maxillary teeth. These teeth have basically the same shape as the distal dentary teeth (Figs. 7-9), but the ankylosed teeth are better preserved and allow observation of some additional features. The teeth are arranged roughly in two rows, along both the lingual and labial margins of the flat ventral surface of the bone. Anterior to the most anterior visible tooth there is a large inflation of the bone, approximately 19 mm long and 17.4 mm wide. This is caused by a large growing tooth that is still completely inside the bone, but can be seen through a small artificial hole in the bone tissue. Therefore, tooth replacement was extralveolar and the new tooth did not shed the old tooth from below.

The labial row has five teeth which are ankylosed to the bone. The tooth row appears to be slightly sinusoidal, with a larger tooth alternating with a smaller one. Teeth are directed labioventrally, and their wear facets also face labioventrally. The crown of tooth 2 is globular, longer (15.75 mm) than wide (12.5 mm), and low (9 mm, but it is slightly deformed). The tip of the crown is worn and shows an elliptical apical wear facet. The crown of tooth 4 is also longer (12 mm) than wide (9.2 mm), and its apical half has been completely worn away. The crown of tooth 5 (21 mm long, about 12 mm wide) is artificially broken. Only the lowermost part of the internal core of the crown remains of the naturally broken tooth 7. Only the mesial half of tooth 9 is preserved and can be seen in cross-section. The base is exposed in linguoventral view only; it is not hollow inside and has an asymmetrical de-

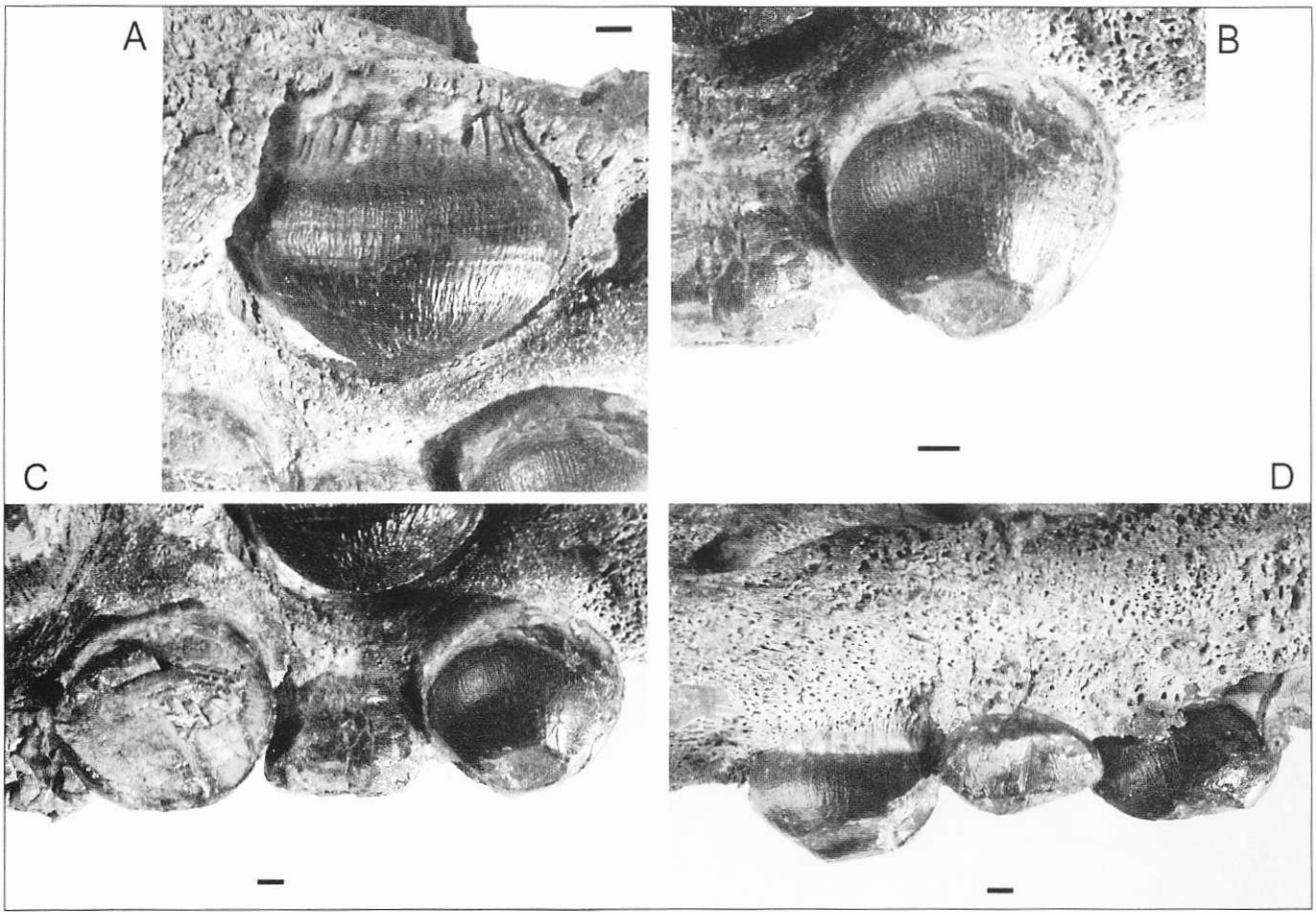

Fig. 9 - MGC 332390, *Tholodus schmidi*. Maxillary teeth. A, tooth 3, lingual view; B, tooth 2, ventral view; C, teeth 2-5, ventral view; D, teeth 2-5, dorsolabial view. Scale bar is 2 mm.

velopment. The crown is apically worn, with an elliptical wear facet. It has a wide pulp cavity filled by carbonate sand because the apical part was originally pierced. The dentine of the crown is thick ventrolingually, and above all dorsolabially, and is thinner toward the base and the apex on the ventrolingual side (Fig. 5B). Between teeth 7 and 9 there is a remnant of a possible old and nearly completely worn tooth.

The base is visible on the labial side of teeth 2 and 5, whereas on the lingual side the base is completely inside the bone. In the smaller teeth 4 and 9 this pattern seems to occur in an opposite fashion (Figs. 9C-D). The bases of teeth 2 and 5 are both surrounded along the lingual side by a smooth band that probably corresponds to cementum or dense attachment bone (cf. tooth 8 of the lower jaw).

The crown surface ornamentation is fainter in the ankylosed teeth than in the alveolate teeth. In particular, the basoapical wrinkles are thinner and the transverse (equatorial) grooves are much less marked (Fig. 9B). The worn or broken crowns show a very thin black layer of enamel, no pulp cavity (excluding tooth 9), and no inner layering of the dentine like that observed in mandibular tooth 3.

The lingual row preserves the evidence of four teeth. Tooth positions 1 and 6 are represented by relatively deep sockets that I consider empty alveoli (Figs. 7A, 8A). That of tooth 1 is 9.5 mm long, 9.1 mm wide and about 5 mm deep; that of tooth 6 is 19 mm long, about 15 mm wide and is comparatively deeper than that of tooth 1 (depth is approximately 15 mm). The lingual alveolar wall of tooth 6 is decidedly lower than the labial wall. Tooth 3 is complete and preserved in its alveolus, but is broken at the upper part of the base, and rotated in a way to expose the lingual side. In this view the basal part is composed of an external "fence" of 13-15 tubular structures, which are hollow with an open inner side, thus resembling in cross-section an upsidedown U, like in the single isolated tooth of the lower jaw. The inner side of the base appears to be hollow. The crown is longer (18.5 mm) than wide (about 11 mm), and is 11 mm high with a pointed, unworn apex (Figs. 7A, 8A and 9A). The superficial ornamentation is the same as that of mandibular tooth 9. The alveolus is larger than the tooth, which probably was not fully functional yet. The lingual wall of the alveolus is decidedly lower than the labial wall (but possibly it has been partly damaged because it is rather thin). Only the base and the basal part of a naturally broken crown of

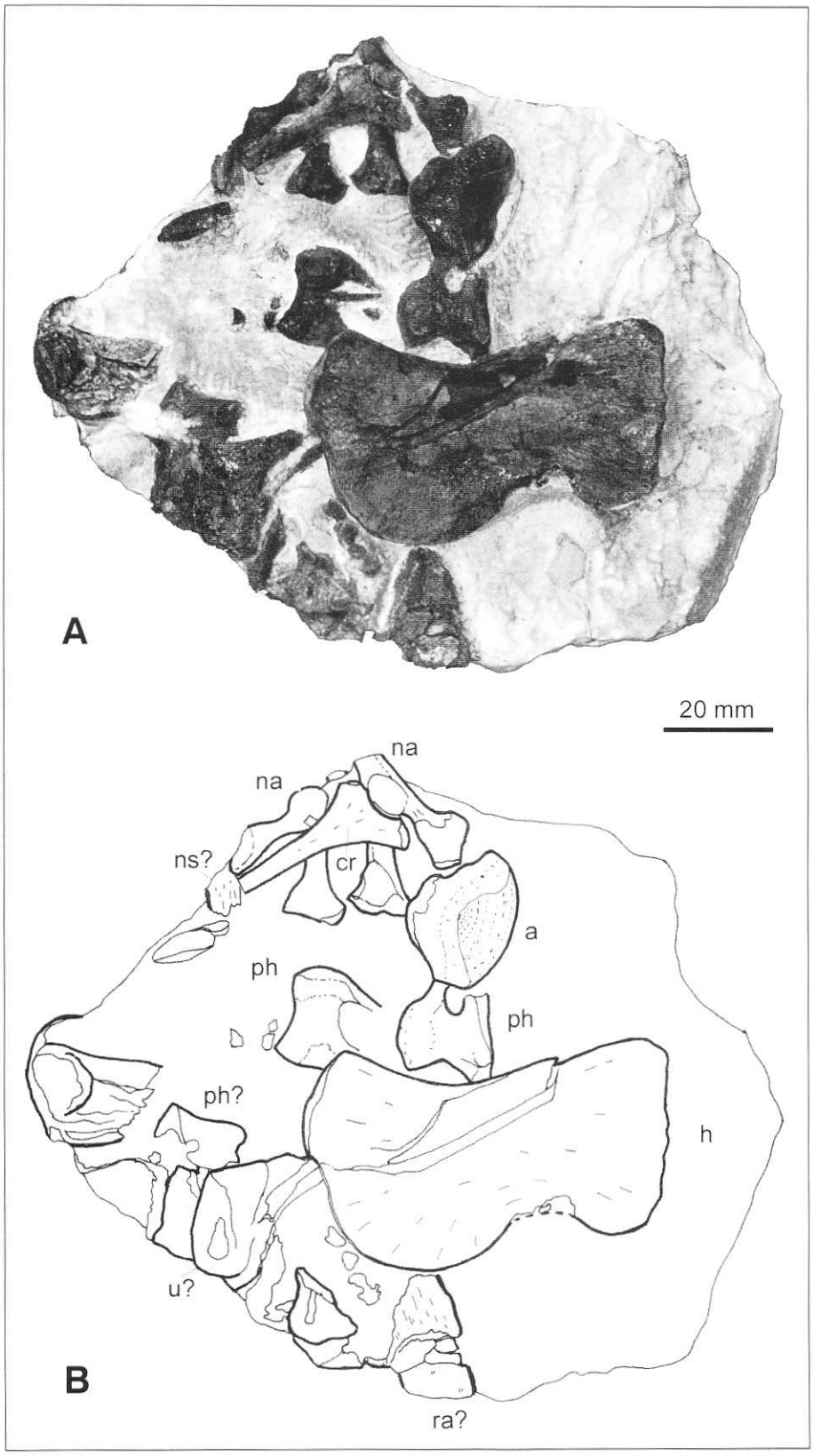

Fig. 10 - MGC 332391, ichthyosaurian remains. A, photograph; B, interpretative drawing. Scale bar is 20 mm. Abbreviations: a, atlas centrum; cr, cervical rib; h, humerus; na, neural arch; ns, neural spine; ph, manual phalanx or metacarpal; u, ulna; ra, radius.

the posterior tooth (8) are preserved. It is ventrolabially directed like the corresponding tooth of the other row (tooth 9). A tangential section of the fluted base is seen at the artificial end of the bone. The base is relatively deeply rooted in the bone (Fig. 5B). The basal part of the broken crown was hollow, as it has been filled by sediment. Thus there was a large pulp cavity. The dentine surrounding the cavity at the base of the crown was thin, like that seen in the ventrolingual side of tooth 9. This tooth was functional and was broken before sedimentation occurred.

Excluding tooth 8, the lingual "alveolate" teeth are never fully grown or are represented by empty alveoli. The fully grown and worn "ankylosed" teeth are placed labially.

The second specimen

Specimen MGC 332391 was found less than 1 metre from MGC 332390 (Mario Campibelli, pers. comm.) in the same rock bed. As far as it can be seen in the field (pers. obs.), MGC 332391 likely came from the same level as MGC 332390. The lithology of the two samples analyzed in thin section is identical.

A complete humerus, a vertebral centrum, two neural arches, a cervical rib, two spool-shaped bones (possibly metacarpals or phalanges, see below), possible fragmentary radius and ulna, and a dozen unidentifiable bone fragments are preserved (Fig. 10). The assemblage of disarticulated bones was partly freed from the limestone in order to identify the single elements.

The left humerus is exposed in ventral view (Fig. 10). It is much longer than wide (length/width ratio = 1.61), its length is 72.5 mm and the maximum width is 45 mm. There is a large, thin bony flange projecting from the shaft anteriorly, which has a notch in the middle-proximal part of its anterior margin. The bone is slightly damaged

around the notch, where the bone is very thin. The margins of the two parts of the flange separated by the notch are rounded. The mediodistal part of the posterior margin of the shaft is concave, and becomes slightly convex proximally. The proximal face is flat anteriorly and slightly concave posteriorly, without a raised head. The ventral part of the proximal margin posterior to the deltopectoral crest is slightly thickened. A deltopectoral ridge runs posterodistally from a knob-like deltopectoral crest. A fracture slightly displaces the posterodistal part of the humerus, and in particular the portion bearing the ulnar facet, which results in an artificial posterolateral projection. The ulnar facet is anteroposteriorly shorter (18.7 mm) than the radial (20.9 mm) and both are low (8 mm is the maximum height) and lozenge-shaped. The posterodistal tuberosity is not well pronounced.

The only vertebral centrum has a circular outline. It is deeply concave on one side and strongly convex on the other. The diameter of the concave side is 28 mm. The convex side is nipple-shaped and has an eccentric notch (Fig. 10). The upsidedown Y-shaped neural arches are close to each other and both preserve only the basal part of the neural spine (Fig. 10). The articular facets of the zygapophyses are horizontal. The cross-section of the apically incomplete spine is rectangular, and is longer than wide. An incomplete rib (34.3 mm long, the distal portion is missing) is double headed, with a long tuberculum (Fig. 10). The shaft is straight and tapers distally; the proximal height is 8 mm, whereas it is only 4 mm at the broken distal end. Two spool-shaped bones with a flat ?proximal and a convex ?distal articular surfaces are preserved close to each other and to the humerus (Fig. 10). They are 18.6 and 20.2 mm long, respectively. A third one is poorly preserved. Both long margins are concave, but one is more concave than the other, nearly circular in one case, due to the presence of two flanges projecting from the proximal and distal extremities. Thus, the bones are C-shaped. Among the poorly preserved bones near the humerus there are probably the proximal parts of the left radius and ulna.

Geological setting

The two specimens MGC 332390 and MGC 332391, were collected at the top of the left flank of Loofs Creek (Rio dai Loofs), about 300 m south-east of Plan Cocés (Fig. 1). The small outcrop is composed of dark gray, rarely pink-spotted, massive limestone, locally very rich in ammonoids and with films of iron oxides. Both specimens, MGC 332390 and MGC 332391, are preserved in fossiliferous wackestone locally rich in thinly-shelled pelagic bivalves, with nodosariid foraminifers and thin films of iron oxides. This microfacies is characteristic of pelagic swells and resembles that of the "*Posidonia*" limestone or the Ammonitico Rosso (Sandro Venturini, pers. comm.).

According to Carulli et al. (1987) the outcrop belongs to the Dont or M. Bivera Formations, indicated by the same colour in the geological map because of their limited thickness. These formations are well-exposed along Ambruseit Creek (Rio dell'Ambruseit), close to the Plan Cocés site (Fig. 1). The underlying Dont Formation is represented there by about 8 m of well-bedded black shales, dark gray limestone and dark gray nodular limestone. The M. Bivera Formation shows, from the bottom to the top, reddish siltstone and marly limestone, with thin layers of lighter nodular limestone regularly bedded; massive reddish marly limestone becoming black upward; well-bedded black limestone, and marly limestone. The thickness of this section is at least 20 m. The Dont Formation there has yielded ammonoids indicative of the *Balatonicus* Subzone (sensu Mietto & Manfrin 1995), Pelsonian, late Anisian (Stefano Manfrin and Paolo Mietto, pers. comm.). Remains of the ichthyosaur *Mixosaurus* sp. have been collected in the section (Rieppel & Dalla Vecchia 2001). According to Farabegoli et al. (1984) the M. Bivera Formation corresponds to the middle-upper part of the *Trinodosus* Zone (early Illyrian, late Anisian).

None of the facies of the Dont Formation-M. Bivera Formation of the Ambruseit Creek resembles that of Plan Cocés site.To solve the problem of dating, the limestone at Plan Cocés immediately below the bone-bearing level was sampled for ammonoids. The sample contains *Balatonites* sp., *Bulogites* sp., "*Ceratites*" *evolvens* Hauer, and *Ptychites* sp., supporting an attribution to the *Balatonicus* Subzone (Stefano Manfrin and Paolo Mietto, pers. comm.), the second of the three Pelsonian ammonoid subzones according to Mietto & Manfrin (1995).

Discussion

The shape, surface ornamentation, pattern of wear and inner structure of the crowns, the fluting of the tooth base, the double rows of teeth in some parts of the lower jaw and maxilla, the irregular arrangement of teeth, and the modality of tooth implantation correspond with those characteristic of *Tholodus schmidi* as described by Peyer (1939; cf. figs. 1, 3, 13, 5-6, 20-21, pls I-II) and Sander & Mazin (1993, pp. 145-147, fig. 1). The mesiodistal crown length is at the lower limit of the range for *Tholodus* crown "diameter" (18-28 mm according to Sander & Mazin 1993). The isolated tooth is probably shed from a more mesial position along the lower jaw with respect to the preserved portion, as it can be seen in the jaw fragment figured by v. Meyer (1851, pl. 31, figs. 27-28).

The mandibular portion from Plan Cocés belongs to an animal with a mandible relatively low dorsoventrally and slender, unlike the deep bone of *Tholodus* that Peyer (1939, fig. 5) identified as a "left dentary", which, however, could be another dentigerous bone. Ornamentation of the crown surface in MGC 332390 is less marked than

that of specimens figured in pls. 1-2 of Peyer (1939), but ornamentation in the specimen figured by Sander & Mazin (1993, fig. 1A-B) has an intermediate relief. Thus this character has probably a certain degree of intraspecific (topological, individual, ontogenetic or sexual) variability.

Tooth implantation in the posterior part of the lower jaw and in the maxilla of the new specimen of *Tholodus* is relatively complex because it varies according to the position of the tooth. The isolated, probable mesial mandibular tooth had a thecodont (or "ichthyosaurian thecodont" according to Motani 1997b, p. 88) implantation. The "alveolate" teeth are in sockets which have a lower lingual wall. Excluding the posterior tooth 8, they are represented only by empty, relatively deep sockets, without any traces of ankylosis of the base, or by non-completely erupted teeth apparently set in deep alveoli larger than the tooth crown. Maxillary tooth 8, which seems to be a fully grown tooth, has a base relatively deeply rooted in the bone and ankylosed, although the upper part is exposed. This resembles the ankylosed thecodont condition of Motani (1997b). Some "ankylosed" teeth have a base slightly rooted inside the bone and not simply leaning above it. The condition of mandibular tooth 8 suggests that the lingual margin of the base was fixed above the lingual margin of a shallow socket, whereas the labial side of the base fused to the labial wall of the socket.

The taxonomic attribution of *Tholodus* is debated. The different taxonomic interpretations must be briefly discussed to understand the nature of the problem. H. v. Meyer (1851) noted that the base of the *Tholodus* tooth resembles that of "labyrinthodont" amphibians and ichthyosaurs, but considered *Tholodus* a fish. Peyer (1939) considered *Tholodus* a squamate or a "rhynchocephalian" reptile, because of the pleurodont-acrodont tooth implantation and the shape of the maxilla. Kuhn (1969) attributed it to the Suborder Claraziasauroidea of the Order Rhynchocephalia (= Sphenodontia), stressing consequently a close relationship of *Tholodus* with Clarazidae (*Clarazia* and *Hescheleria*), one of two families of the Claraziasauroidea, along with Tholodontidae. Kuhn (*ibidem*) considered as acrodont the tooth implantation of *Tholodus*. *Clarazia* and *Hescheleria* are now considered to belong to Thalattosauria, an incertae sedis group nested in the Neodiapsida (Rieppel 1987). The shape of the lower jaw and the arrangement of the mandibular bones in *Clarazia* are different than in MGC 332390 (Rieppel 1987). The maxilla of *Clarazia* has only a tooth row, and tooth implantation "if not fully acrodont, shows a marked reduction of the "angle of pleurodonty"" (Rieppel 1987, p. 109). The lower and upper jaw of *Hescheleria* and its dentition clearly differ from that of MGC 332390 (ibidem).

Tholodus is not a sauropterygian, as tooth implantation and replacement differ from that seen in this group (Rieppel 2001).

According to Smith Woodward (1932), *Tholodus* is an ichthyosaur of the family Omphalosauridae. Romer (1956) considered it as a possible synomym of the Early to Middle Triassic *Omphalosaurus* Merriam, which he placed as an ichthyosaur close to *Grippia* and possibly to *Torectonemus*. Lucas (1997), Sander & Mazin (1993), Sander & Faber (1998), and Sander (2000) also considered *Tholodus* to be an ichthyosaur. However, it has not been mentioned in recent reviews of Triassic ichthyosaurs (Callaway & Massare 1989; Mazin 1986; Motani 1999b; Maisch & Matzke 2000). It is unclear whether this is because the authors do not consider it an ichthyosaur, or that they simply decided to ignore it because of its scanty record and ambiguous identification. It is a fact that none of the nine unambiguous diagnostic features of Ichthyopterygia listed by Motani (1999b), and none of the seven diagnostic features of Ichthyosauria of Maisch & Matzke (2000) can be checked on the material of *Tholodus*. Sander & Mazin (1993) also considered *Tholodus* as closely related to *Omphalosaurus*. However, Motani (2000) explicitly argues against the inclusion of *Omphalosaurus* in Ichthyosauria. *Omphalosaurus* differs in many respects from *Tholodus*, namely in the shape and size of the teeth, their arrangement and distribution in the dentigerous bones, the peculiar shape of the dental batteries, the absence of infolding of the dentine in the tooth bases (Sander & Mazin 1993; Sander & Faber 1998; Motani 2000) and in enamel microstructure (Sander 1996). The shared features are highly convergent characters, such as the presence of teeth with a rounded crown and multiple tooth rows (Motani 2000). In particular *Omphalosaurus* lacks an important feature present in both ichthyosaurs and *Tholodus*: the folded dentine in the tooth base (plicidentine). Plicidentine is a common feature of ichthyosaur teeth (Peyer, 1968) and is possibly an autapomorphy of the clade (Motani 1999b, 2000). Therefore, the exclusion of *Tholodus* from Ichthyosauria is in any case not justified by the sole supposed affinity to *Omphalosaurus*.

In addition to the plicidentine, tooth implantation of the Italian *Tholodus* specimen is more reminiscent of the relatively complex tooth implantation present in Triassic ichthyosaurs (Motani 1997b) than the simple acrodont implantation in sphenodontians, or the pleurodont implantation of most squamates. Also, the slender lower jaw and the arrangement of the mandibular bones of MGC 332390 are similar to the condition in ichthyosaurs (Motani 1999b; Maisch & Matzke 2000) and bones undoubtedly referable to an ichthyosaur have been collected close to it (see below).

My conclusion is that *Tholodus* is not a squamate, a sphenodontian, or a claraziid thalattosaurian, and the ichthyosaur attribution remains the most plausible.

The tooth shape and arrangement along the lower jaw of MGC 332390 has some resemblance to those of the Triassic ichthyosaurs *Phalarodon nordenskioeldii*

(Hulke) and *Chaohusaurus geishanensis* Young & Dong, as shown in lateral view reconstructions of the skull and lower jaw by Maisch & Matzke (2000, figs. 1-4). However, teeth of *Phalarodon nordenskioeldii* are very narrow labiolingually and mesiodistally elongated (Maisch & Matzke 2000, fig. 17), unlike those of *Tholodus*. *Chaohusaurus geishanensis* (Early Triassic, China) has five rounded and blunt distal mandibular teeth preceded by teeth with an apparently pagoda-like crown. Pagoda-like crowns are present also in the maxilla. "Posterior teeth labio-lingually wide, and swollen in lateral view" is a diagnostic feature of the genus (Motani & You 1998, p. 533). Posterior dentary teeth of *Chaohusaurus* are only slightly longer mesiodistally than labiolingually (ibidem), like those of *Tholodus*. *Chaohusaurus* does not seem to have more than two rows of posterior teeth (Motani & You 1998, fig. 2), although Maisch & Matzke (2000, p. 61) quote "several maxillary tooth rows" as a diagnostic character of the genus. According to Maisch & Matzke (2000) it belongs to the clade Grippiidae, whose members share the following synapomorphies: 1) posterior tooth crowns rounded, 2) tooth size relative to skull width small (< 0.05), 3) maxillary tooth row multiple (ibidem, p. 94). *Tholodus* shares characters 1 and 3, but probably not character 2. The clade Grippida of Motani (1999b, p. 477) includes the same taxa as Grippiidae and is diagnosed by "posterior tooth crowns rounded, multiple maxillary tooth rows". According to Sander & Mazin (1993, p. 147), *Grippia*, the only other member of Grippiidae/Grippida, "differs from *Tholodus* in having only two tooth rows in the upper jaw and one in the lower". This is not the case, because *Tholodus* has one or two rows in the posterior part of the lower jaw, depending on the position, and the maxilla has two rows. Unlike those of *Tholodus*, the rounded posterior teeth of *Grippia* are small, and their implantation is subthecodont, and with a different replacement (Motani 1997a, b). The large pulp cavities surrounded by a thin dentine wall, characteristic of *Grippia* according to Motani (1997a, b), is a feature that seems to be present in some teeth of *Tholodus* (maxillar tooth 8 and partly 9 of MGC 332390), but not in other teeth.

The humerus of MGC 332391 strongly resembles that of immature individuals of *Chaohusaurus geishanensis*, especially in the elongation and the outline of the anterior and posterior margins (length/width ~ 1.55 in IVPP V11362) (Motani & You 1998, fig. 1B-C; Motani 1999b, fig. 3). "Anterior flange of the humerus notched, at least in young individuals" is a diagnostic feature of *Chaohusaurus* (Motani & You 1998, pp. 533-534). The humerus of MGC 332391 is much larger than those in known specimens of *Chaohusaurus geishanensis*, and its proximal face is wider and flat. The absence of the caput humeri in MGC 332391 suggests that it was not ossified and that the individual was immature (Johnson1977; Motani & You 1998).

The vertebral centrum resembles the atlantal centrum of the Triassic ichthyosaurs *Utatsusaurus hataii* Shikama, Kamei & Murata and *Cymbospondylus petrinus* Leidy, being peculiarly convex on the cranial side and concave on the caudal side (Merriam 1908; Maisch & Matzke 2000). The rib resembles the posterior cervical ribs of *Cymbospondylus petrinus* (Merriam 1908), and the neural arches are similar to those of the anterior cervicals of this taxon (Merriam 1908). The spool-like elements show some resemblance to the proximal phalanges of basal ichthyosaurs (e.g., Motani 1999a).

It cannot be affirmed without any doubt that MGC 332390 and MGC 332391 belong to the same taxon, because it cannot be proved that they were in articulation or strictly associated. However, there is some evidence suggesting that this could be the case:

1) MGC 332391 is an ichthyosaur, as shown mainly by the humerus, but also by the axial centrum, the cervical rib and the neural arches. The humerus strongly resembles that of immature specimens of *Chaohusaurus*. *Tholodus* is considered an ichthyosaur by many authors. It has a relatively slender lower jaw and a fluted tooth base as do ichthyosaurs, and a dentition which resembles that of *Chaohusaurus* in some respects;

2) The ichthyosaurian remains belong to an immature individual and the teeth of *Tholodus* from Alps are at the lower limit of the size range of those found in the Muschelkalk Basin;

3) The specimens were found close to each other, probably in the same level (the two rock samples show the same microfacies), and they are the only vertebrate remains found in the outcrop;

4) Vertebrates are very rare in the Triassic pelagic units of Udine Province (Sirna et al. 1994). It seems unlikely that two specimens found so close to each other could belong to different individuals and different taxa gathered this way by chance.

It must be also observed that pelagic (i.e. far from coastal influence) formations mainly contain remains of reptiles well-adapted to aquatic life, namely ichthyosaurs, during Middle Triassic times. This is the case for all Triassic basinal units of NE Italy (Sirna et al. 1994; Rieppel & Dalla Vecchia 2001; pers. obs.).

The above observations suggest that *Tholodus* may be an ichthyosaur similar to *Chaohusaurus*, although more evidence is needed to confirm this hypothesis.

Stratigraphic remarks

Despite its debated taxonomic identity, *Tholodus* is considered a good index fossil in the biostratigraphy of Muschelkalk Basin, because it occurs only in the lower Muschelkalk (Hagdorn 1993; Lucas 1997; Hagdorn & Rieppel 1999). Most *Tholodus* specimens have been found in the Terebratelbänke (= *Terebratula* Beds or Terebratelbank Subformation in Hagdorn & Rieppel 1999) of the Jena Formation (upper Lower Muschelkalk, Pelsonian,

Decurtella decurtata Biozone) from Tatzende near Jena (Thuringia, central Germany), the type locality where specimens described by Meyer (1851) come from, and in the Schaumkalkbänke (Schaumkalkbank Subformation in Hagdorn & Rieppel 1999) (upper Lower Muschelkalk, uppermost Pelsonian/lower Illyrian, *Judicarites* and *Neoschizodus orbicularis* assemblage zone) near Freyburg on River Unstrut (Saxony-Anhalt) (the specimens described by Jaekel 1907; Fritsch 1906; Sander & Mazin 1993). One tooth and a fragmentary dentigerous bone, both still undescribed, come, respectively, from the Terebratelbänke of Bödigheim near Buchen (Baden-Württemberg) and of Thuringia (H. Hagdorn, pers. comm.). A dentigerous bone was found in the *Terebratula* Formation (corresponding to the Terebratelbänke of Jena Formation, H. Hagdorn, pers. comm.) of Strzelce Opolskie (once Großstrehlitz) in Silesia (Poland) (Sander & Mazin 1993). A tooth-bearing jaw fragment and some isolated teeth were collected in the lower Wellendolomit (= Frudenstad Formation) of Rohrdorf, Dornhan and Warth near Altensteig (Baden-Württemberg, SW Germany) (Peyer 1939) that may be slightly older than the Terebratelbänke, presumably early Pelsonian or even Bithynian (H. Hagdorn, pers. comm.).

In summary, the stratigraphic range of *Tholodus* falls between the lower Wellendolomit (= Frudenstad Formation) and the Schaumkalkbänke, but most specimens have been found in the Terebratelbänke and in the Schaumkalkbänke of the Jena Formation. Thus the *Tholodus* acme occurs around the maximum flooding surface (corresponding to the Terebratelbänke) of the first Muschelkalk sequence (M1) (Hagdorn & Rieppel 1999). This narrow range induced Hagdorn (1993) and Hagdorn & Rieppel (1999) to establish a *Tholodus* biozone (Total Range Biozone) in a scheme of Reptile Biozonation for the marine Middle Triassic of the Germanic Basin. The *Tholodus* biozone represents the upper part of the lower Muschelkalk (Pelsonian-lower Illyrian of the Tethyan Standard Chronostratigraphic Scale) (Hagdorn & Rieppel 1999). The validity of this biozone was contested by Lucas (1997, p. 429) because it "does not correspond to the stratigraphic range of *Tholodus*". According to Hagdorn & Rieppel (1999, p. 672) the comment by Lucas is based on the fact that "*Tholodus* has a wider stratigraphic range in North America than the Germanic Muschelkalk *Tholodus* biozone". Actually Lucas (1997) does not mention any North American *Tholodus* specimens and his comment probably refers to the German specimens from the Wellendolomit that are possibly slightly older than Pelsonian.

The Pelsonian dating of the specimen from the Southern Alps is in agreement with the distribution of the genus in Central Europe and confirms the relatively short stratigraphic range of *Tholodus*, suggesting the validity of this taxon as an index fossil outside the Muschelkalk basin.

Conclusions

Tholodus is for the first time reported outside the Anisian of Central Europe, showing that it is not endemic to the Muschelkalk Basin. Its relatively short stratigraphic range (Pelsonian-early Illyrian) is confirmed. Crowns of the mesial mandibular teeth are pagoda-like and apicobasally higher than mesiodistally long, whereas those in a more distal position are longer than high like the maxillary ones. Tooth implantation is rather complex, unlike the simple acrodont implantation of sphenodontians or the pleurodont one of many squamates. The dentition of *Tholodus* shows some resemblance to the dentition of Early-Middle Triassic grippiid ichthyosaurs. The dentary, splenial, surangular, and angular are anteroposteriorly elongated bones and their positions resemble those of the slender lower jaw of ichthyosaurs. Remains of an ichthyosaur resembling *Chaohusaurus* are associated, but not articulated, to *Tholodus* dentigerous bones, and suggest that *Tholodus* might be a grippiid ichthyosaur close to *Chaohusaurus*. This must be confirmed by more material in anatomical articulation. In any case, a further form is added to the ichthyosaur taxa recently reported from the Middle Triassic of Udine Province: *Mixosaurus* Baur, *Cymbospondylus* Leidy, and possibly *Shastasaurus* Merriam (Rieppel & Dalla Vecchia 2001), showing a relatively high local diversity.

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