Paläontologische Zeitschrift	71 (3/4)	267–289	8 Abb., 1 Tab.	Stuttgart, Oktober 1997

Mikadocephalus gracilirostris n. gen., n. sp., a new ichthyosaur from the Grenzbitumenzone (Anisian-Ladinian) of Monte San Giorgio (Switzerland)

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With 8 figures and 1 table

Kurzfassung: Ein nahezu vollständiger Schädel eines neuen Ichthyosauriers aus der mitteltriassischen Grenzbitumenzone vom Monte San Giorgio (Kanton Tessin, Schweiz) stellt einen der vollständigsten und besterhaltenen Funde des Schädels eines großwüchsigen triassischen Ichthyosauriers dar, die bisher bekannt wurden. Die Beziehungen zu anderen triassischen Ichthyosaurier-Taxa werden diskutiert, und es wird gezeigt, daß der Fund einer neuen Gattung und Art angehört, *Mikadocephalus gracilirostris*, die sich aber keiner der gegenwärtig anerkannten Familien triassischer Ichthyosaurier zuordnen läßt. Große Ähnlichkeiten im Schädelbau bestehen zu den posttriassischen Ichthyosauriern, mit denen eine Reihe wichtiger apomorpher Merkmale geteilt werden.

Abstract: An almost complete skull of a new ichthyosaur from the Middle Triassic Grenzbitumenzone Beds of Monte San Giorgio (Kanton Tessin, Switzerland) represents one of the most complete and best preserved finds of a large Triassic ichthyosaur cranium. Its affinites with other Triassic ichthyosaur taxa are discussed and it is demonstrated to represent a new genus and species, *Mikadocephalus gracilirostris*, which does not fit into any of the currently recognized families of Triassic ichthyosaurs. Remarkable similarities in cranial structure exit to post-Triassic ichthyosaurs, with which a number of important apomorphies are shared.

Introduction

The Middle Triassic (Anisian-Ladinian) Grenzbitumenzone of Monte San Giorgio, Kanton Tessin, Switzerland, is well known for its wealth of marine vertebrates and invertebrates (PEYER 1944; KUHN-SCHNYDER 1973). It consists of a series of alternating dolomite layers and bituminous shales of moderate thickness (about 16 m at the Cava Tre Fontane locality, RIEBER 1973), which crops out in the area south of lake Lugano, including localities in Northern Italy (BASSANI 1886; REPOSSI 1902). The presence of ichthyosaurs had been noticed in the first half of the 19th century but none were described until 1886 when the Milan palaeontologist FRANCESCO BASSANI gave a short diagnosis of a new species, *Ichthyosaurus cornalianus*, based on material from Besano in Northern Italy (BASSANI 1886). It was due to the insight of BAUR (1887) that this animal was recognized as representing a distinct ichthyosaurian genus showing primitive features in the limb skeleton not found in any Jurassic form. BAUR named the taxon *Mixosaurus*. The rich collections of *Mixosaurus* from Monte San Giorgio made by the Palaeontological Institute of the Universität Zürich since 1924 have never been described but are currently under study by Dr. W. BRINKMANN (Zürich). The only further contributions to the knowledge of the osteology of this ichthyosaur were made by VON HUENE, based on a small sample of well preserved material in the collection of the Institut und Museum für Geologie und Paläontologie der Universität Tübingen (GPIT) (VON HUENE 1916, 1925, 1936, 1949), and by BESMER (1947), a student of BERNHARD PEYER, who published an extensive dissertation on the dentition of ichthyosaurs, including material from Monte San Giorgio. BRINKMANN (1996) identified the first embryos in a Triassic ichthyosaur in a specimen of *Mixosaurus cornalianus*.

SANDER (1989) described a new ichthyosaur from Monte San Giorgio on the basis of an almost complete skeleton already noted by KUHN-SCHNYDER (1963, 1973), as a new species of the genus *Cymbospondylus* LEIDY 1868. *Cymbospondylus buchseri* SANDER 1989 is quite different from the American type-species of the genus, *Cymbospondylus petrinus* LEIDY 1868. SANDER noted the presence of two other ichthyosaur taxa in the collection from Monte San Giorgio, one of them smaller, the other one even larger than *Cymbospondylus buchseri*.

The purpose of this paper is to describe a third ichthyosaur taxon from Monte San Giorgio on the basis of a fairly complete and excellently preserved, but very disarticulated skull and mandible in the collection of the GPIT. It is intermediate in size between *Mixosaurus cornalianus* and *Cymbospondylus buchseri*, and although it shares several primitive features with each of these taxa, it shows peculiarities of cranial osteology and a combination of

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0031–0220/97/0071–0267 $ 5.75

cranial characters not found in these or any other hithero known Triassic ichthyosaur. It is consequently referred to a new genus and species.

Abbreviations

Al, Alveoli; Ang, Angular; Ar, Articular; Bsp, Basisphenoid; C, Condylus; Cf, Carotid foramen; Cor, Coronoid; Ept, Epipterygoid; F, Frontal; Fqj, Facet for the quadratojugale; Fsa, Foramen surangulare; J, Jugal; L, Lacrimal; La, Lamina ascendens; Mx, Maxilla; Mxg, Maxillar groove; N, Nasal; P, Parietal; Pal, Palatine; Pc, Processus coronoideus; Pcf, Processus cultriformis; Pf, Parietalforamen; Pmx, Praemaxilla; Pnp, Postnarial process of the maxilla; Pof, Postfrontal; Pq, Processus quadratus; Pra, Praearticular; Prf, Praefrontal; Psp, Parasphenoid; Pt, Pterygoid; Q, Quadrate; Qj, Quadratojugal; Sa, Surangular; Sc, Sclerotic plates; So, Supraoccipital; Spl, Splenial; Sq, Squamosum; St, Supratemporal; Sta, Stapes; Tpq, Triangular projection of the quadrate; V, Vomer.

Systematic Palaeontology

Tetrapoda incertae sedis

The systematic position of the ichthyosaurs is still controversial. Whereas some authors (TARSITANO 1982, 1983; MASSARE & CALLAWAY 1990; CALDWELL 1996) advocate a diapsid origin of ichthyosaurs, others (RIESS 1986; MAISCH in press) go as far as to question even the amniote status of ichthyosaurs. It is therefore considered best, at least for the moment, to leave this question open to discussion.

Order Ichthyosauria DE BLAINVILLE 1835
Family not designated (terminal taxon)

As is shown in the comparative section below, the new specimen can not be referred to any currently recognized genus of Triassic ichthyosaur, nor does it exclusively share any derived features with shastasaurids, mixosaurids or omphalosaurids, which are the three currently recognized families of Triassic ichthyosaurs. It shares, however, a number of important cranial characters with post-Triassic ichthyosaurs, possibly representing the sister-group of the post-Triassic forms. Since the new taxon does not form a monophyletic group with any other hitherto known ichthyosaur, instead representing a monospecific terminal taxon, we consider it redundant to erect a new family for its reception at the moment.

Genus *Mikadocephalus* n. gen.

Type species: *Mikadocephalus gracilirostris* n. gen., n. sp.
Derivatio nominis: Mikado (Jap.) - literally: the venerable gate; originally honourable name for the Japanese emperor, nowadays mainly referring to the well-known Mikado-game; kephalos (Greek) – head. Chosen for the resemblance of the scattered and superimposed cranial bones of the holotype skull to a heap of Mikado-sticks.

Diagnosis (including autapomorphic and plesiomorphic features): Large ichthyosaur; skull length > 50 cm; snout length ca. 66 % skull length; snout exceedingly slender and gracile; orbital diameter ca. 20 % skull length; postorbital skull segment ca. 13 % skull length; temporal fenestra large, > 50 % orbital length; naris bordered by maxilla, premaxilla and nasal; probably no posterodorsal premaxillary process; maxilla with long and slender postnarial process, tooth row only extending up to this process; nasal reaching far anteriorly and posteriorly, very slender; frontal small, bordering parietal foramen only anteriorly, excluded from temporal fenestra; postfrontal with well developed posterolateral process taking part in anterior and anterolateral margin of temporal fenestra; quadratojugal with long, clearly offset processus quadratus and long anterodorsal extension; supratemporal with low anterior horizontal ramus, large posterior flange covering quadrate well developed; parabasisphenoid with small slit-like paired openings for internal carotid arteries separated by posterior extension of parasphenoid, processus cultriformis very slender, without ventral ridge; quadrate with pronounced ventromedial corner; pterygoid slender and narrow, indicating large interpterygoid vacuities, quadrate process elongated and slender, no posteromedial process overlying basioccipital; upper teeth small, widely spaced, mostly slender, only posteriormost maxillary teeth somewhat shortened and of larger diameter, but never blunt, anterior maxillary teeth set in distinct alveoli, posterior teeth situated in continuous groove, surangular with a big and well developed coronoid process.

Possible autapomorphies of *Mikadocephalus* are:
1. Exceedingly slender and gracile snout;
2. Presence of triangular medioventral process on quadrate;
3. Very large and well developed coronoid process on surangular;
4. Elongated quadrate process of pterygoid;
5. Maxillary teeth thecodont anteriorly, aulacodont posteriorly;
6. Large size.

Mikadocephalus gracilirostris n. sp.

Derivatio nominis: gracilis (lat.) gracile or slender, rostrum (lat.) snout; referring to the exceedingly slender snout region of the animal's skull.
Holotype: Figs. 1-7 (GPIT 1793/ 1).
Locus typicus: Monte San Giorgio, Kanton Tessin, Switzerland.
Stratum typicum: Grenzbitumenzone Beds, Anisian-Ladinian, Middle Triassic.

Diagnosis: As for genus, since it is the only species currently recognized.

Description

Preservation

The specimen is preserved in three slabs of bituminous shale (Figs 1,2), which can be fitted together quite precisely. The skull has undergone strong maceration and dislocation. Most of the cranial elements are, however, preserved in a satisfactory state. As is usual in the fossiliferous strata of Monte San Giorgio, the individual skull bones are strongly compressed and have also often undergone three-dimensional deformation due to the superposition of several elements. Original preparation was done purely mechanical in a rather crude manner, yielding only badly exposed or even damaged bone surfaces in many areas. Repreparation of the specimen was accomplished by Mr. FRITZ

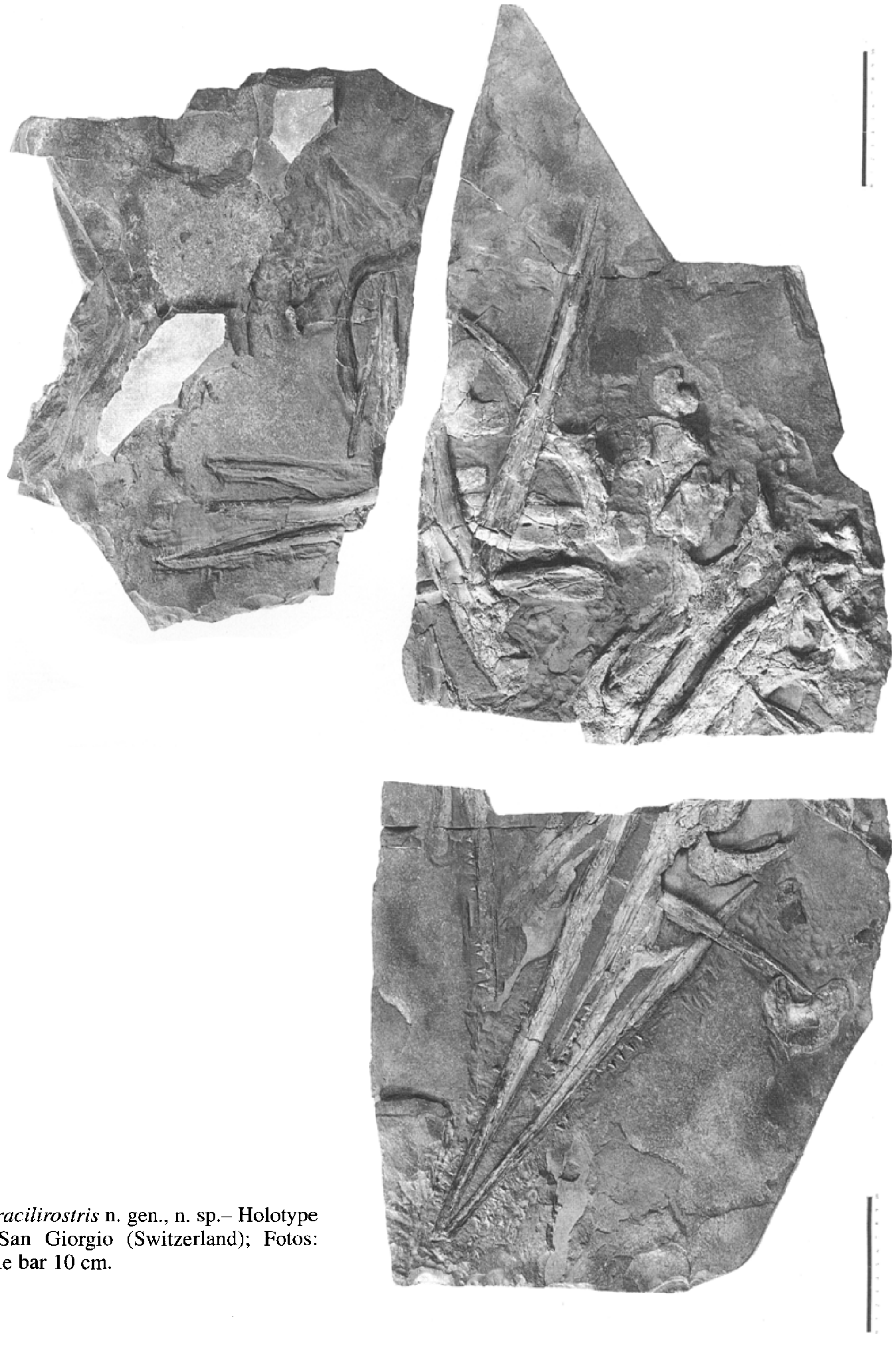


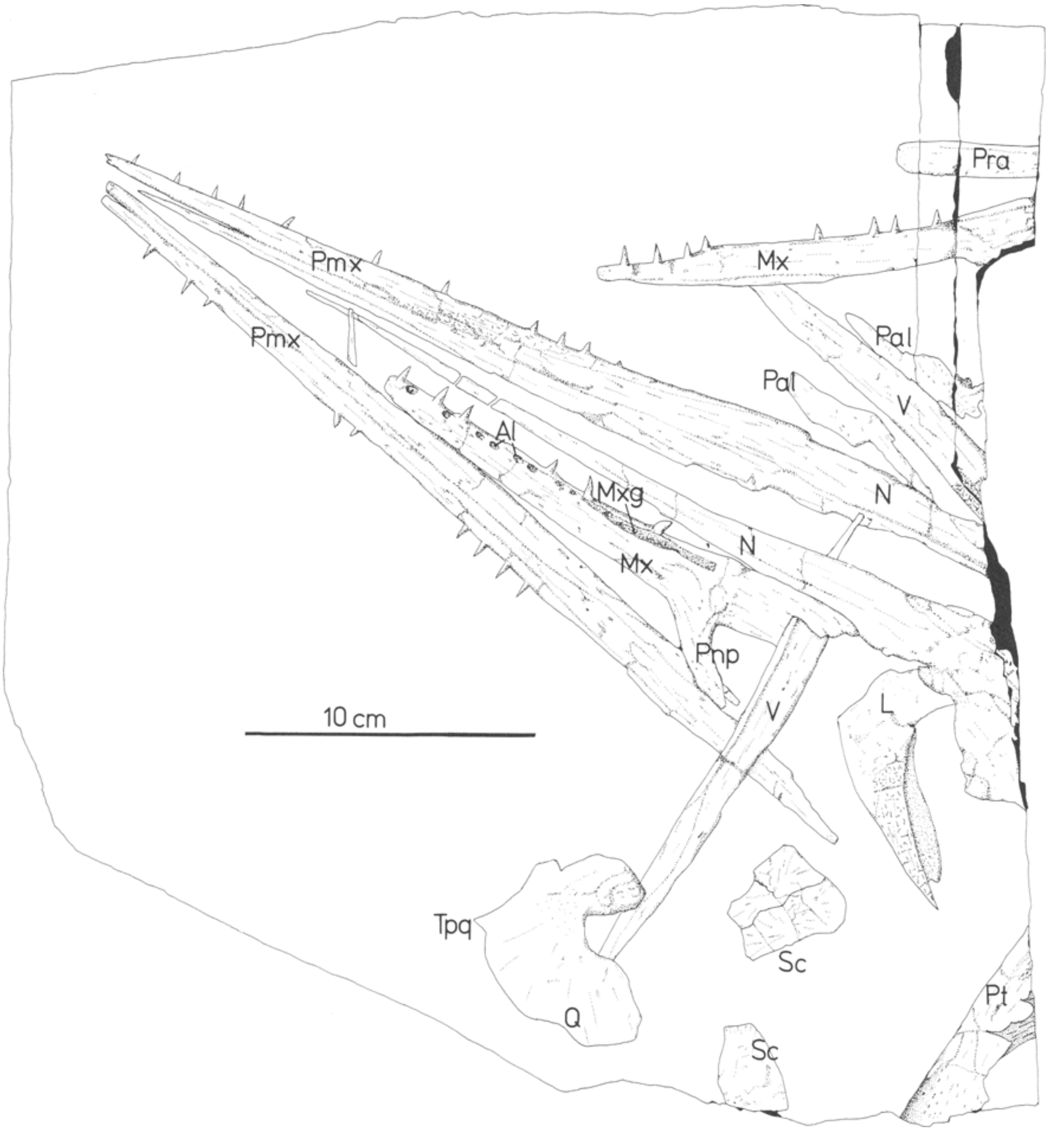
Fig. 1. *Mikadocephalus gracilirostris* n. gen., n. sp.– Holotype (GPIT 1793/1), Monte San Giorgio (Switzerland); Fotos: GERBER (Tübingen).– Scale bar 10 cm.

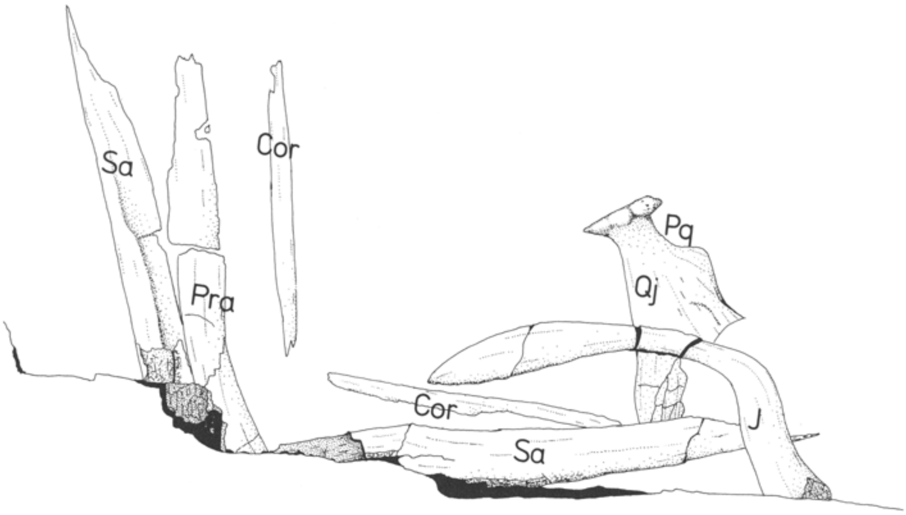
LÖRCHER (Dotternhausen) with the aid of a self-constructed air abrasive device. The specimen is now excellently developed and shows even minutest sutural and surface details.

Elements of the dermatocranium

Premaxilla: Both premaxillae are preserved almost completely. They are exposed in internal view. The premaxilla is obviously much more elongated and of more gracile build than in any other adequately known large Triassic ichthyosaur. Anteriorly it is produced into a blunt and very low tip. It becomes gradually higher posteriorly by means of a thin dorsal lamella, which does not extend up to the preserved posterior end of the bone, but terminates some 7 cm in front of it in the form of a short pointed process, which defines the anterior border of the external narial opening (observable on left premaxilla). The posteriormost part of the premaxilla thus forms a low and very delicate process ventrally, representing the processus subnarialis. The short pointed supranarial process has no

Fig. 2. *Mikadocephalus gracilirostris* n. gen., n. sp. – Holotype (GPIT 1793/1).– For abbreviations see text.–

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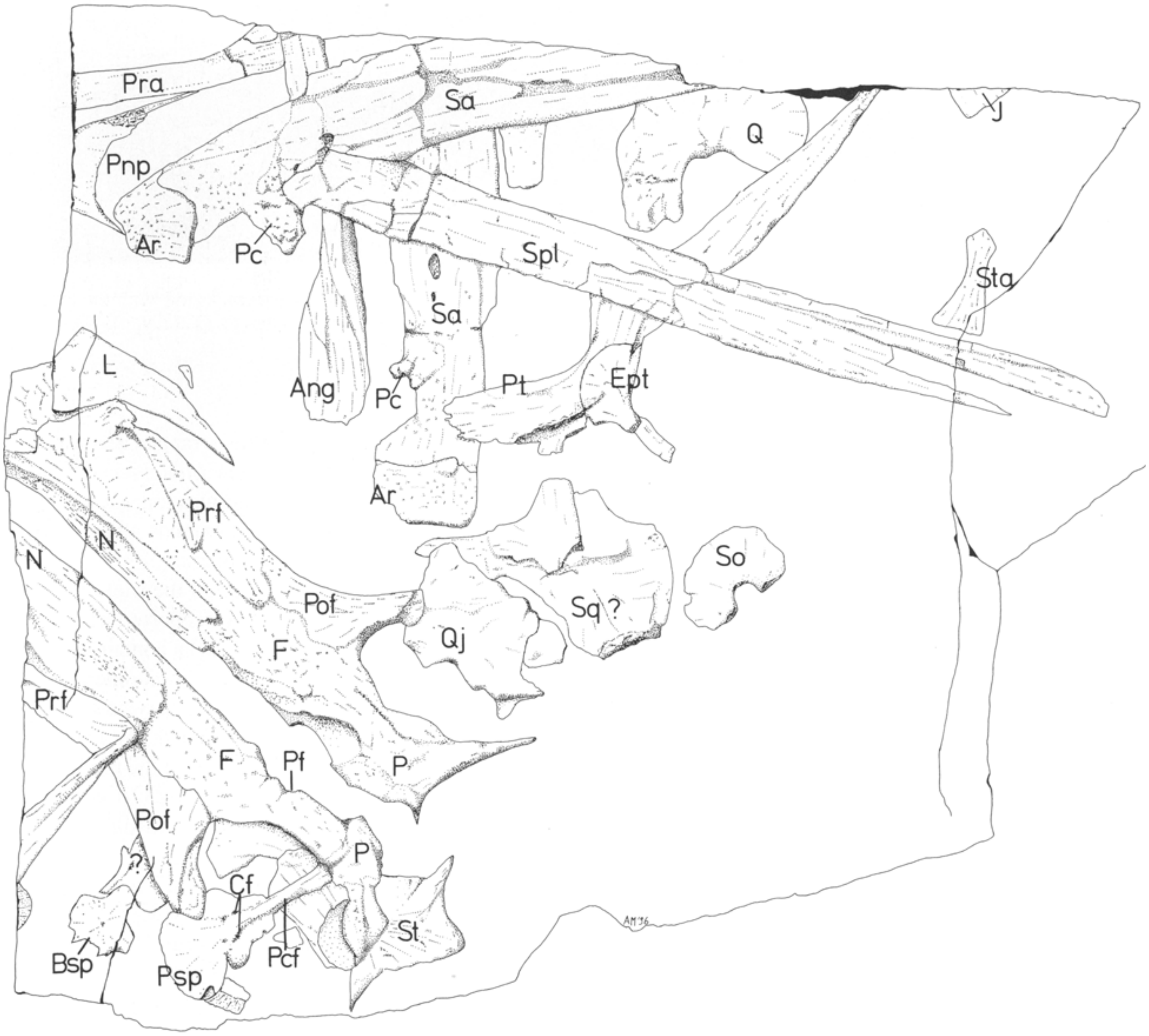
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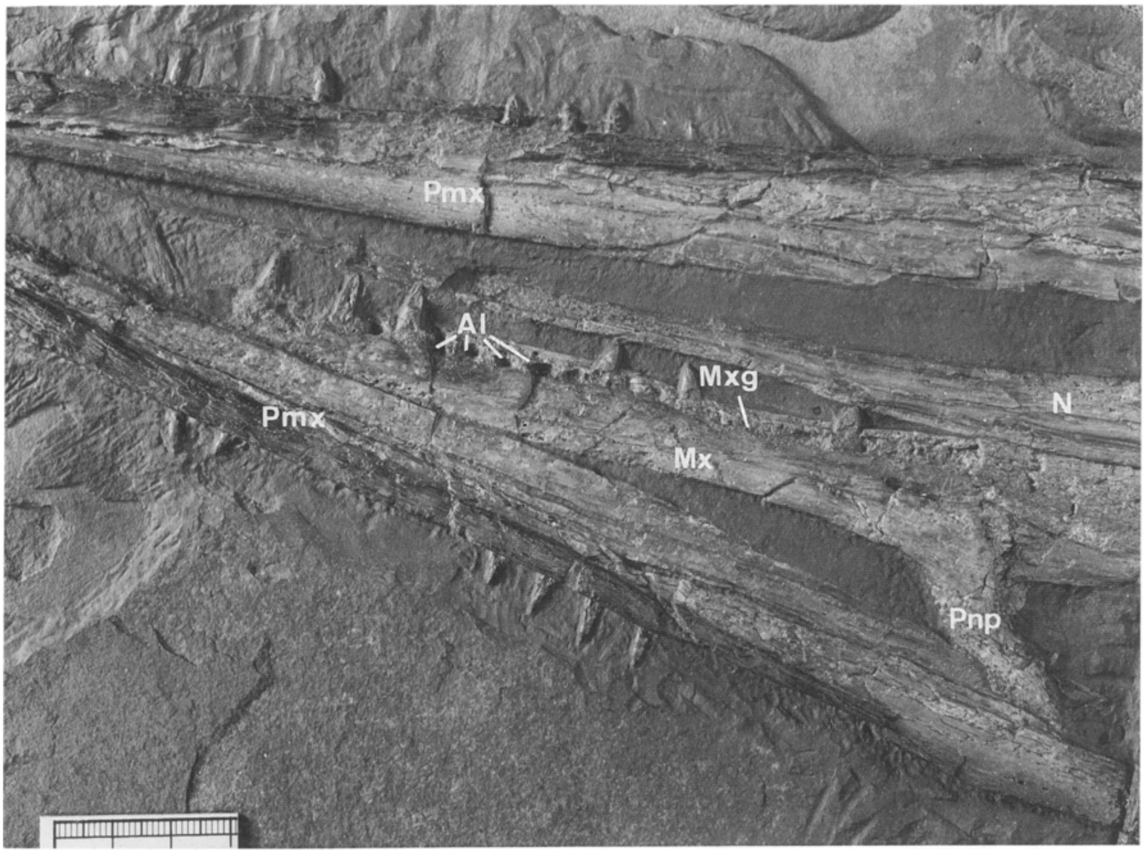

Fig. 3. *Mikadocephalus gracilirostris* n. gen., n. sp.– Holotype (GPIT 1793/1). Right maxilla in external view with the long and slender postnarial process, maxillary teeth thecodont anteriorly and aulacodont posteriorly. Foto: GERBER (Tübingen).– For abbreviations see text.– One unit of the scale bar: 10 mm.

resemblance to the very long and elongated structure found autapomorphously in shastasaurs (CALLAWAY & MASSARE 1989b; MASSARE & CALLAWAY 1990). The ventral tooth bearing margin of the premaxilla is thickened. The ventral margin, which is perfectly straight for its entire length, also thins out posterior to the preserved tooth row. This indicates that the extent of the premaxillary dentition -and therefore the amount of overlap between premaxilla and maxilla- can be adequately estimated (Fig.3). The internal surface of the premaxilla bears a deep groove situated just dorsal to the thickened toothbearing margin. In the anterior third of the premaxilla, the bone dorsal to that groove is also of quite robust build. The thinner dorsal lamella bears a system of smaller longitudinal grooves and ridges. Posterior to the tooth row the right premaxilla shows a probable facet for the anterior end of the vomer, bordered for its entire length by the ventral thickened margin of the premaxilla ventrally and -at least anteriorly- by a somewhat pronounced ridge of the medial surface dorsally. The dorsal and posterior margins of both premaxillae are not preserved completely.

The premaxilla contacts the nasal medially and the maxilla posteriorly. It is certainly excluded by the postnarial process of the maxilla from contact with the lacrimal. The premaxilla formed the entire anterior part of the dorsal and probably most of the ventral border of the external narial opening. The premaxilla was thus arranged in a way very similar to Jurassic taxa such as *Stenopterygius* (VON HUENE 1922; pers. obs.), i. e. sending a long slender processus subnarialis backwards that extends along the ventral border of the external narial opening.

Teeth are preserved from the tip of the snout for a distance of approximately 20 cm. Further posteriorly no teeth can be identified. The right premaxilla contains 9 recognizable teeth, 12 can be seen in its left counterpart. The last 4 teeth of the right premaxilla are very probably representing a complete segment of the tooth row (Fig.3) and allow a rough estimate of the number of the premaxillary teeth, which must have come close to 25. It is not clear how these teeth are attached to the premaxilla.

Maxilla: Both maxillae are preserved. The right maxilla (Fig.3), which is exposed in external view, is almost complete with only the posterior tip missing. The left maxilla, showing its internal aspect, is strongly damaged in the postnarial region. The tooth-bearing parts of both maxillae are well preserved. The maxilla is essentially a triradiate bone with a long and slender anterior tooth-bearing and probably shorter and relatively high plate-like posterior part (Fig.3). At about two thirds of the bone's length, a posterodorsally directed, long and slender postnarial process (Fig.3) is developed, which borders the lacrimal anteriorly, thus excluding it from the narial margin. This process is a feature of most Triassic ichthyosaurs, seen in taxa such as *Mixosaurus* (VON HUENE 1916, 1925, 1936, 1949; pers. obs.) or *Cymbospondylus* (MERRIAM 1908; SANDER 1989; MASSARE & CALLAWAY 1990). In contrast to other adequately known Triassic ichthyosaurs the process is very long and strongly recurved (the curvature might be exaggerated due to deformation), which indicates that the maxilla most probably established contact with the prefrontal, as is also the case in *Mixosaurus* (VON HUENE 1925, 1936; pers. obs.). Anteriorly the maxilla terminates in a bluntly rounded tip. The maxilla definitely forms the entire posterior border of the external naris. Posterior to the postnarial process the maxilla is not well preserved on either side. The dorsalmost part of the posterior extension is made up of a slightly depressed area that exhibits a smooth surface, probably the facet for the lacrimal.

The maxillary dentition consists of 6 preserved teeth in the right (Fig.3) and 8 in the left maxilla. The tooth-bearing margin of the right maxilla is completely exposed due to deformation. The anterior teeth are seen to be set in distinct alveoli (Fig.3). This is definitely true for the first 15 tooth positions. Further posteriorly the alveoli become less well defined and at least the posteriormost 30% of the tooth row are entirely aulacodontous (Fig.3) (MAZIN 1983).

The posteriormost teeth are situated anterior to the postnarial process.The dental groove extends to the level of the postnarial process, yielding further evidence for the lack of teeth in the posterior portion of the maxilla. The same feature is observable to a variable extent in *Cymbospondylus* (MERRIAM 1908; SANDER 1989).

Nasal: The right nasal is almost completely preserved and exposed from its ventral side. It is still in natural articulation with the frontal and prefrontal. The left nasal is also still in natural articulation posteriorly, but very incomplete and heavily damaged, not showing any additional features. The extremely gracile nasals are separated along the midline. They taper out anteriorly to an exceedingly narrow and thin strip (Fig.3), which indicates that there was no major overlap of the premaxilla onto the nasal. Where the nasal contributes to the dorsal margin of the external naris, its lateral rim shows a slight but distinct step. This is, after a distance of only about 2 cm, followed by an even more pronounced and apparently slightly thickened lateral extension, which probably intruded into the dorsal narial margin.

Further posteriorly where the nasal forms part of the skull roof proper, it is very tightly sandwiched in between the prefrontal, laterally, and the frontal, posteriorly. The naso-frontal suture is complicated, being serrate and extending transversely in its lateral portion, running longitudinally further medially, with the nasal apparently sending a long narrow process posteriorly. It is, however, very probable that this impression is a result of extensive overlap of the nasal onto the anterior portion of the frontal. This is observable in many post-Triassic ichthyosaurs, e.g. *Ichthyosaurus* (SOLLAS 1916; MC GOWAN 1973) and *Stenopterygius* (GODEFROIT 1993, 1994; pers. obs.). Only the most medial portion of the posterior end of the nasal would thus be exposed ventrally. Even though there is no direct evidence for this assumption, the arrangement of the skull roof bones observable in the specimen renders it very probable. A remarkable feature of the internal surface of the nasal is the presence of a strong longitudinal parasagittal ridge, which extends along the whole length of the element, becoming higher and broader posteriorly. The specimen definitely lacks the contacts between nasal and postfrontal and nasal and supratemporal, described in *Cymbospondylus* (MERRIAM 1908; SANDER 1989).

Frontal: Both of the approximately quadrangular frontals are preserved in ventral view, retaining their natural position with the surrounding skull roof elements. As with the nasals they are split along the midline. The right frontal is almost completely preserved. The anterior part of the left frontal is partially hidden below the nasal and the prefrontal. At its anterior margin there is a major ventral overlap with the nasal, as described above. The lateral suture with the prefrontal and the postfrontal is strongly serrate and takes a sigmoidal course. These two bones exclude the frontal from the margin of the orbit. The frontal underlaps the parietal ventrally (Fig.6), the bones forming a strongly interdigitating suture. An anterolateral process of the parietal meets the postfrontal (Fig.6) and definitely excludes the frontal from the temporal opening, as in post-Triassic ichthyosaurs such as *Ichthyosaurus* (SOLLAS 1916; MC GOWAN 1973) and *Stenopterygius* (VON HUENE 1922; pers. obs.). The ventral surface of the frontal is very cancellous, bearing numerous pits and hollows (Fig.6). Two short parasagittal longitudinal grooves are seen on the underside of the right frontal. The interfrontal suture is straight, lacking any definite embayment for the parietal foramen. The frontal forms merely the anterior margin of the parietal foramen (Fig.6), as e.g. in *Shonisaurus* (CAMP 1980) and *Thaisaurus chonglakmanii* (MAZIN et al. 1991). On the left side the posteriormost portion of the frontal is broken off, exposing the parietal, which in dorsal view of the skull roof must have formed practically the entire margin of the parietal foramen. A distinct ovoid facet is shown on the undersurface of the parietal where the frontal is missing (Fig.6).

The most distinctive feature of the frontal is its small size and minor contribution to the dorsal skull roof, approaching the condition seen in post-Triassic ichthyosaurs (OWEN 1881; SOLLAS 1916; VON HUENE 1922; MC GOWAN 1973) but contrasting with that usually present in Triassic forms (MERRIAM 1908; VON HUENE 1916).

Parietal: The almost complete parietals are preserved in natural position and seen in ventral view (Fig.6). They are anteroposteriorly elongated bony plates bordered by the frontals, anteriorly, and forming most of the medial as well as part of the posterior margin of the temporal fenestrae.

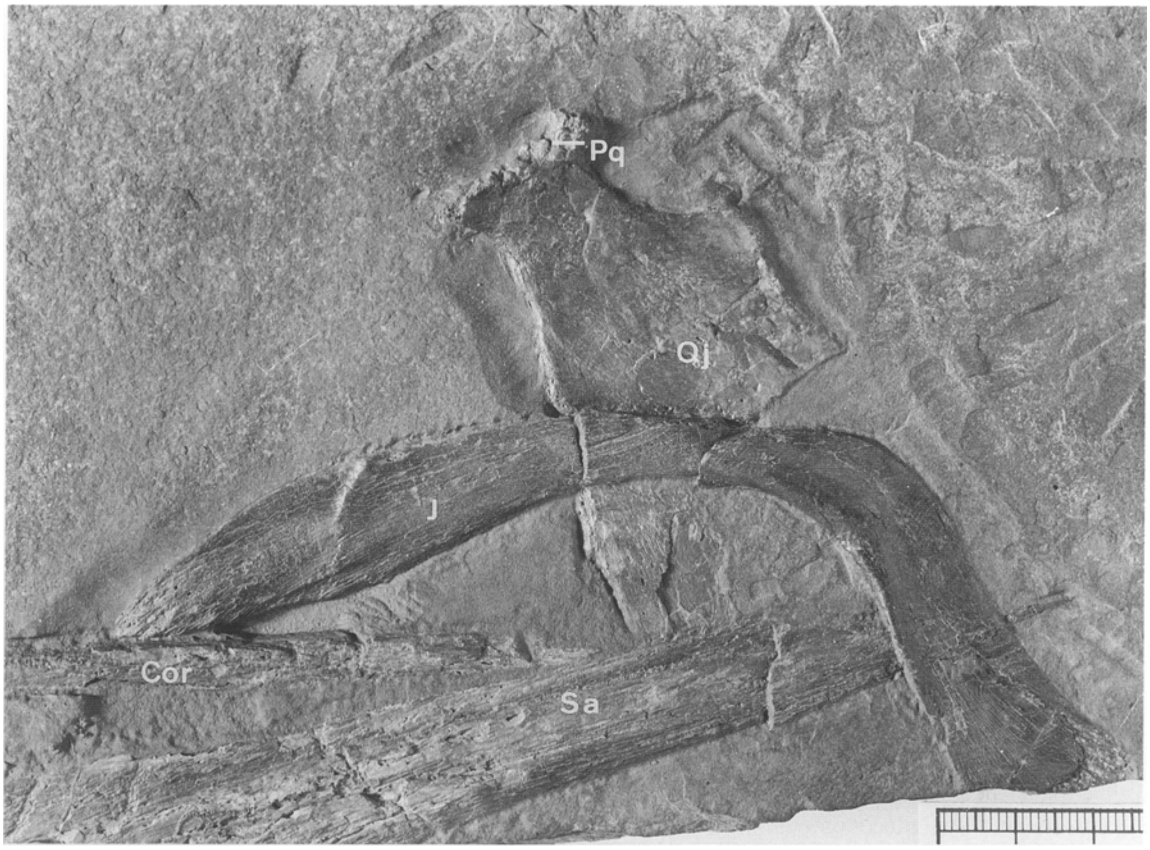

Fig. 4. *Mikadocephalus gracilirostris* n. gen., n. sp.- Holotype (GPIT 1793/1). Right quadratojugal in internal view with the prominent processus quadratus, left jugal in internal view. Foto: GERBER (Tübingen).- For abbreviations see text.- One unit of the scale bar: 10 mm.

In contrast to the mixosaurids, the temporal fenestra was definitely not a small slit-like aperture but rather a subrectangular, well-developed opening, probably as big as in the Lower Liassic *Stenopterygius* (VON HUENE 1922; GODEFROIT 1993, 1994; pers. obs.). An anterolateral process forms part of the anterior temporal margin and contacts the postfrontal (Fig.6). A narrow vertical flange extends posterolaterally, probably contacting the occipital ramus of the supratemporal and thus contributing to the posterior temporal margin. The interparietal suture shows a distinct embayment in its anterior third, which is interpreted as the lateral border of the parietal foramen, which was thus enclosed mainly within the parietals.

There is no indication of a ventral parietal flange which, in *Ichthyosaurus* (MC GOWAN 1973), contacts the epipterygoid. It is probably crushed beyond recognition. Along the lateral margin of the left parietal a deep groove is running for almost the entire length of the bone (Fig.6). It could mark the course of a major blood vessel, possibly the vena capitis dorsalis.The posterior margin of each parietal is running obliquely to the long axis of the skull at an angle of ca. 45 ° (Fig.6), similar to the situation in *Ichthyosaurus* (SOLLAS 1916; MC GOWAN 1973).

Supratemporal: The structure of the temporal region of ichthyosaurs has long been debated. MAISCH & HUNGERBÜHLER (in press) have recently demonstrated that the interpretation of BAUR (1887) and VON HUENE (1916, 1922), who identified three bones in the temporal region, the uppermost of which represents an unusually complex supratemporal, is the most plausible. The situation in *Ichthyosaurus* (MC GOWAN 1973) and *Platypterygius* (ROMER 1968), where the squamosal is lost or fused to the quadratojugal, must then be considered as autapomorphic for these taxa. In Triassic ichthyosaurs a supratemporal has been identified in *Mixosaurus* (VON HUENE 1916, 1925, 1936, 1949; pers. obs.), *Grippia* (MASSARE & CALLAWAY 1990) and *Cymbospondylus petrinus* (MERRIAM 1908; VON HUENE 1916) amongst others.

In the new specimen only the right supratemporal (Fig.6) can be confidently identified. It lies adjacent to the right parietal but has been rotated, so that it shows its posterior and dorsal rather than ventral and anterior surface as would be expected. The left supratemporal is absent. As in post-Triassic forms the supratemporal is a complex element. An anterior horizontal process, definitely taking part in the formation of the lateral temporal margin, is developed as a low, vertical plate of bone most of which is unfortunately broken off. A posteromedial process of roughly triangular shape probably established contact with the posterolateral process of the parietal. It is not well preserved and its margins are damaged. Bad preservation of the supratemporal and the parietal does therefore not allow to establish the exact nature of this contact.

The supratemporal shows a very large posteroventral flange of rounded outline (Fig.6), which probably covered large parts of the quadrate medially as in *Ichthyosaurus* (Mc Gowan 1973) and *Stenopterygius* (pers. obs.). It is very similar in size, shape and proportions to the same flange in a well preserved skull of *Stenopterygius longifrons* (Owen 1881) in the GPIT collection (GPIT 1576). In *Cymbospondylus petrinus*, the only known Triassic ichthyosaur in which the occiput is adequately preserved, the posteroventral supratemporal flange is only of very modest size (Merriam 1908; Camp 1980).

? Squamosal: The squamosal can not be identified with a large degree of confidence. It might be represented by a roughly triangular plate of bone lying in close proximity to the left quadratojugal from which a long -and presumably ventral- process, the margins of which are largely broken, is extending. If this hypothesis is accepted, the left squamosal would be exposed in internal view. The (?) posterior margin is strongly damaged in its dorsal portion, but satisfactorily preserved further ventrally, not showing any sutural surfaces, which indicates that it formed the posterior margin of the skull in that area. If this was the case, the squamosal would have to wrap around the posterodorsal corner of the skull for a considerable distance, since the presumed posterior margin is deeply concave. The dorsal (?) margin would be rather straight anteroposteriorly, whereas the (?) anteroventral margin takes a gently posteroventrally curving course, as far as it is preserved. If this was the correct orientation, the squamosal would have a general shape resembling that seen in *Stenopterygius* (pers. obs.) and *Temnodontosaurus* (Maisch & Hungerbühler in press), but would come even closer -being in fact almost identical- to the squamosal of a yet undescribed ichthyosaur from the Posidonia Shales of Holzmaden (Maisch in prep.). We do not know of any other bone in either the cranial or postcranial skeleton of ichthyosaurs, which resembles the questionable element more closely.

Quadratojugal: Both quadratojugals are preserved as isolated elements. The left quadratojugal is showing its external aspect but has suffered much from inadequate original preparation. The right quadratojugal (Fig.4), the internal side of which is exposed, is, however, complete and excellently preserved.

The element has the shape of a subrectangular plate from which two processes extend. A long and broad, very thin plate extends from the anterodorsal corner of the bone. It might have intruded some distance between the postorbital and squamosal as in *Temnodontosaurus* (Maisch & Hungerbühler in press), but preservation is not adequate to establish this beyond doubt. Posteroventrally the quadratojugal is produced into a very prominent processus quadratus (Fig.4) (Sollas 1916), which is clearly offset from the main body of the bone and bears a thickened, dorsoventrally elongated facet for contact with the quadrate. The prominence and distinctive morphology of this process recalls that of *Cymbospondylus* (Merriam 1908; von Huene 1916), *Ichthyosaurus* (Conybeare 1822; Sollas 1916) and *Temnodontosaurus* (Fraas 1913), *Parvinatator wapitiensis* (Nicholls & Brinkman 1995) but it is quite different from the much smaller and less distinct process in more advanced post-Triassic forms such as *Stenopterygius* (pers. obs.) and *Ophthalmosaurus* (Andrews 1910). The anteroventral margin of the quadratojugal is slightly thickened and somewhat concave (Fig.4), whereas the posterodorsal margin, as far as it can be observed, is practically straight.

Lacrimal: Both lacrimals are preserved close to their natural position and both are exposed from their internal side. The lacrimal is a posteriorly curving element of approximately droplike shape, possessing a broadened anterior part and a long and slender posteroventral suborbital process, which is visible almost entirely in the right lacrimal, being compressed in approximately the same plane as the rest of the bone The suborbital process is a very thin and narrow bony plate, showing a clear facet for reception of the anterior spur of the jugal ventrally. The dorsal part of the left lacrimal is heavily damaged. The lacrimal contacts the prefrontal only with its posterodorsal extremity, the two bones bordering the anterior margin of the orbita, from which the maxilla and the nasal are thus excluded. The leading edge of the lacrimal possesses a small ledge along its anterior margin not completely preserved on either side, which must have established a somewhat overlapping contact with the postnarial process of the maxilla as it is seen in *Mixosaurus* (von Huene 1916, 1925, 1949; pers. obs.).

Jugal: The left jugal (Fig.4) is excellently preserved as a completely isolated element, showing its internal aspect. It consists of a long, horizontal, anterior, suborbital and shorter, posterior, ascending, postorbital ramus, which are orientated at an angle of about 90°. The suborbital ramus is laterally compressed in its anterior half, forming a rather thin plate of bone, which terminates in a pointed anterior tip (Fig.4). The posterior half of the suborbital ramus is more rounded in cross section and becomes very slender posteriorly, being narrowest at the point of junction with the postorbital ramus (Fig.4). The postorbital ramus is again laterally flattened, with an almost straight anterior and slightly convex posterior margin. Its leading edge bears a low ridge, which tapers out at about half the height of the postorbital ramus. Between this ridge and the posterior margin, the internal surface of the postorbital ramus is slightly concave in its ventral half, but becomes slightly convex further dorsally. There is no posteroventral flange at the junction of suborbital and posterior ramus as in

Cymbospondylus petrinus (MERRIAM 1908; VON HUENE 1916; SANDER 1989). The dorsal margin of the postorbital ramus is almost straight. The dorsalmost portion of the bone is only an exceedingly thin lamella, which was probably overlapped by the postorbital externally to a certain degree. The nature of the contact with the quadratojugal cannot be definitely established. Anteriorly the jugal was probably overlapped externally by the posteroventral suborbital extension of the lacrimal. In turn it might have overlapped the maxilla to some degree. The jugal forms most of the ventral margin of the orbit and also takes part in the formation of the posterior orbital margin. The strong curvature of the entire bone, as well as the morphology of the quadratojugal, strongly suggests that a very pronounced jugal-quadratojugal notch was developed, as it is seen in e.g. *Cymbospondylus petrinus* (MERRIAM 1908), *Parvinatator wapitiensis* (NICHOLLS & BRINKMAN 1995) and *Grippia longirostris* (WIMAN 1928; MAZIN 1981).

Prefrontal: The prefrontals are ventrally exposed in natural articulation. The prefrontal is a narrow, longitudinally elongated element that internally forms at least two thirds of the dorsal orbital margin. Anteriorly it contacts the postnarial portion of the nasal and, as indicated above, might also have established a short contact with the postnarial process of the maxilla. The nature of the contact with the lacrimal is in some doubt, but it was probably also quite short. Medially the prefrontal forms a long contact with the nasal anteriorly and the frontal posteriorly. It contacts the postfrontal in a short transverse interdigitating suture posteriorly.

In ventral view the postfrontal surface is differentiated into two areas. Firstly, a small anteromedial lamella, which lies level with the adjacent interior surfaces of the nasal and frontal and resembles them in texture. This extends only for about half the length of the bone. Secondly, the entire lateral portion of the prefrontal, which parallels the orbital margin, offset from the rest of the internal skull surface by a strong ridge protruding at a maximum of 5 mm at its anterior end. A strong step is thus formed between the anteromedial prefrontal lamella anteriorly, and the internal frontal surface posteriorly, on the one hand, and the lateral elevated prefrontal portion on the other hand. This is similar to the situation in *Ichthyosaurus* (MC GOWAN 1973), where the medial prefrontal lamella, however, extends for the entire length of the bone. The texture of the bone is very different between the two portions, that of the lateral elevated part being less cancellous and bearing a relatively smooth surface. A deep and wide sulcus on the inside of the skull roof is formed between the lateral ridge of the prefrontal laterally and the marked parasagittal medial ridge of the nasal medially. It probably accommodated part of the forebrain, possibly the lobus olfactorius (MC GOWAN 1973).

Postfrontal: Both postfrontals are retaining their natural position within the skull roof and show their ventral aspect. They are posterolaterally curving, elongated and, compared to other well known Triassic taxa such as *Cymbospondylus* (MERRIAM 1908; SANDER 1989) or *Mixosaurus* (VON HUENE 1925; pers. obs.), surprisingly short elements. Medially they contact the frontals in a serrate suture (Fig.6), the amount of overlap between the bones probably being minute. Anteriorly a deeply interdigitating, short transversal suture with the prefrontal is formed. On the right side it is visible that the postfrontal is extending somewhat further anteriorly, overlapping the prefrontal, part of which is broken off. Posteriorly the postfrontal is produced into a narrow, gently curving process (Fig.6), which definitely formed most of the anterior margin of the temporal fenestra. Judging from the small size of the element, it is clear that the postfrontal did not contribute significantly to the lateral margin of the temporal opening, which contrasts with the situation in all other known ichthyosaurs except *Grippia longirostris* (WIMAN 1928) and *Thaisaurus chonglakmanii* (MAZIN et al. 1991). The postfrontal was not totally excluded from the temporal margin, as in the latter species, the situation being most probably quite similar to that in *Grippia*. The posterolateral postfrontal process shows a distinctive sutural facet (Fig.6), probably for reception of the anterior horizontal ramus of the supratemporal.

Posteromedially the anteroventral process of the parietal and the postfrontal show a short but distinct suture (Fig.6), thus entirely excluding the small frontal from the rim of the temporal fenestra. As in all ichthyosaurs the posterior margin of the orbita was formed by the postfrontal and postorbital. The postfrontal in ventral view forms only about one third of the dorsal orbital margin. As indicated above, it is clear that it considerably overlapped the prefrontal dorsally and would -in external view- appear as a much more extensive element.

Postorbital: There is no unequivocal evidence of the postorbital in the specimen.

Palate

? Vomer: Two long and slender, imperfectly preserved bones situated in the snout region of the specimen probably represent the two vomers. They can not belong to the mandible nor do they resemble any other skeletal element. The better preserved of the two is probably the right vomer seen in medial view. It bears much resemblance to the corresponding element in the Middle Jurassic *Ophthalmosaurus icenicus* (ANDREWS 1910), except that it is even more slender and elongate.

The element is a very thin plate, which becomes slightly thicker posteriorly and has a rather pointed anterior end. The posterior margin of the bone is not preserved. The anterior third of the preserved ventral margin is reinforced by a prominent ridge (Fig.7), whereas the dorsal margin is produced into a thin vertical lamella of bone. Further posteriorly, the surface is slightly dorsoventrally concave. The element interpreted as a portion of the left vomer is only an elongate plate of bone with a slightly convex sur-

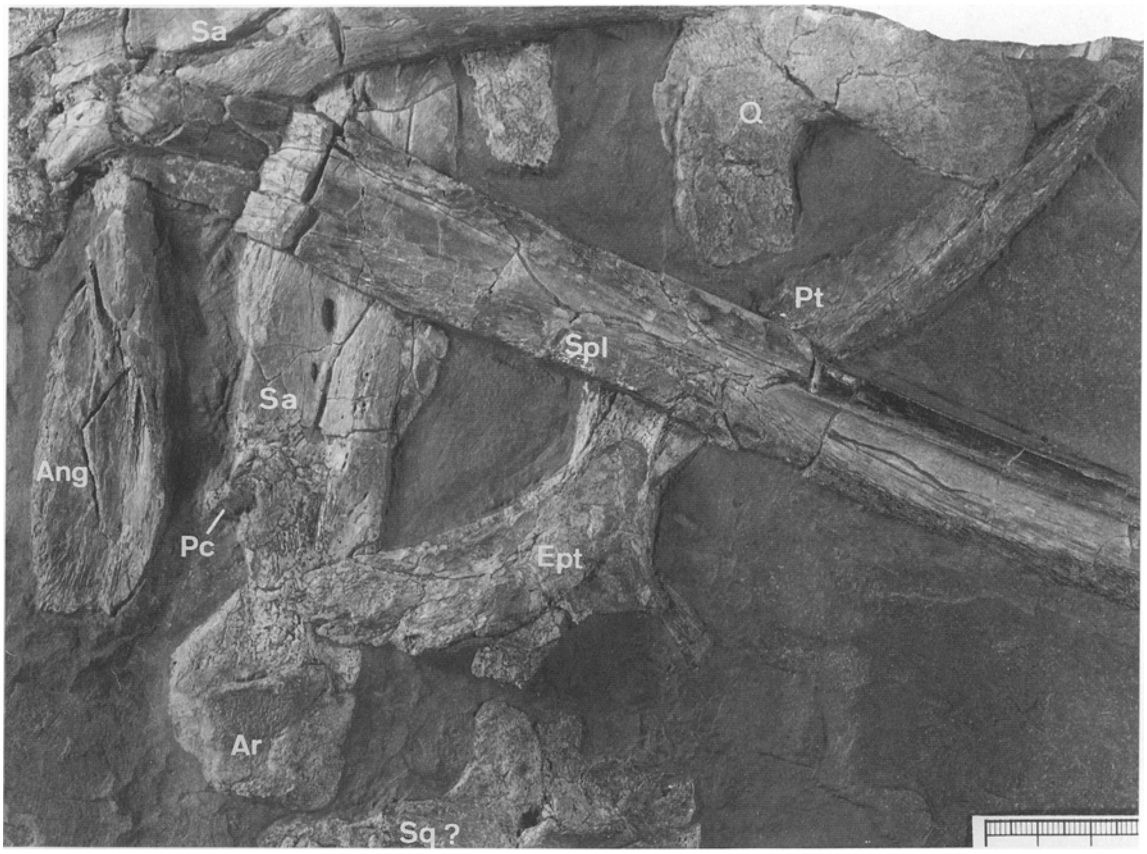

Fig. 5. *Mikadocephalus gracilirostris* n. gen., n. sp.- Holotype (GPIT 1793/1). Pterygoid and epipterygoid in situ, pterygoid with three posterior processes, epipterygoid situated anterior to the lamina ascendens, surangular with very large coronoid process. Foto: GERBER (Tübingen).- For abbreviations see text.- One unit of the scale bar: 10 mm.

face, which might indicate that it is showing its lateral side. It has imperfectly preserved ends and does not show any additional features.

? Palatine: Two small splinters of bone, which lie adjacent to the elongate plate of the (?) left vomer, possibly represent incomplete portions of both palatines as is suggested by their position and shape. They both show very clearly-defined, rounded margins, which are interpreted as parts of the edges of the internal narial openings. They strongly resemble the isolated palatine of *Temnodontosaurus platyodon* described and figured by GODEFROIT (1992). Their small size suggest that large parts of both bones have been lost. That the two bone fragments are almost mirror images of each other indicates that one of them shows its ventral, the other one the dorsal side. The better preserved element is interpreted as the anteriormost portion of the left palatine seen in dorsal view, the anterior tip still pointing anteriorly. The less well preserved element could then only be the right palatine in ventral view, rotated by 180°, with its anterior tip pointing posteriorly.

Pterygoid: The left pterygoid (Fig.5) is completely and excellently preserved, showing its dorsal aspect. Only part of its middle portion is covered by the overlying right splenial (Fig.5). The pterygoid is very pointed anteriorly, being produced into a narrow but robust, slightly medially curving process, getting gradually broader posteriorly. The posterior half of the pterygoid is of complex shape. Its lateral border is deeply emarginated for its entire length. About where the lateral emargination starts, two distinct ridges are developed on the dorsal surface of the bone (Fig.5), which possibly could delimitate an anterior cartilaginous extension of the epipterygoid. At its posterior end the pterygoid is produced into three processes (Fig.5). The lateral quadrate process is an elongate broad plate with a rounded outline. Distally its margins are somewhat damaged. On the dorsal surface a very stong ridge is found anterior to which the epipterygoid is preserved in situ (Fig.5). This structure running straight anteroposteriorly, represents the compressed ascending quadrate process (lamina ascendens) of the pterygoid (ANDREWS 1910; SOLLAS 1916; MC GOWAN 1973). Posteromedially a small bony flange, the medial margin of which is broken, represents the "medial wing" (MC GOWAN 1973), which established contact with the basis cranii. Generally surprising – if one compares well known Triassic taxa such as *Mixosaurus* (VON HUENE 1916), *Shastasaurus* (MERRIAM 1902) and *Cymbospondylus* (MERRIAM 1908) – is the slender and gracile build of the entire pterygoid, which is distinctly different from the

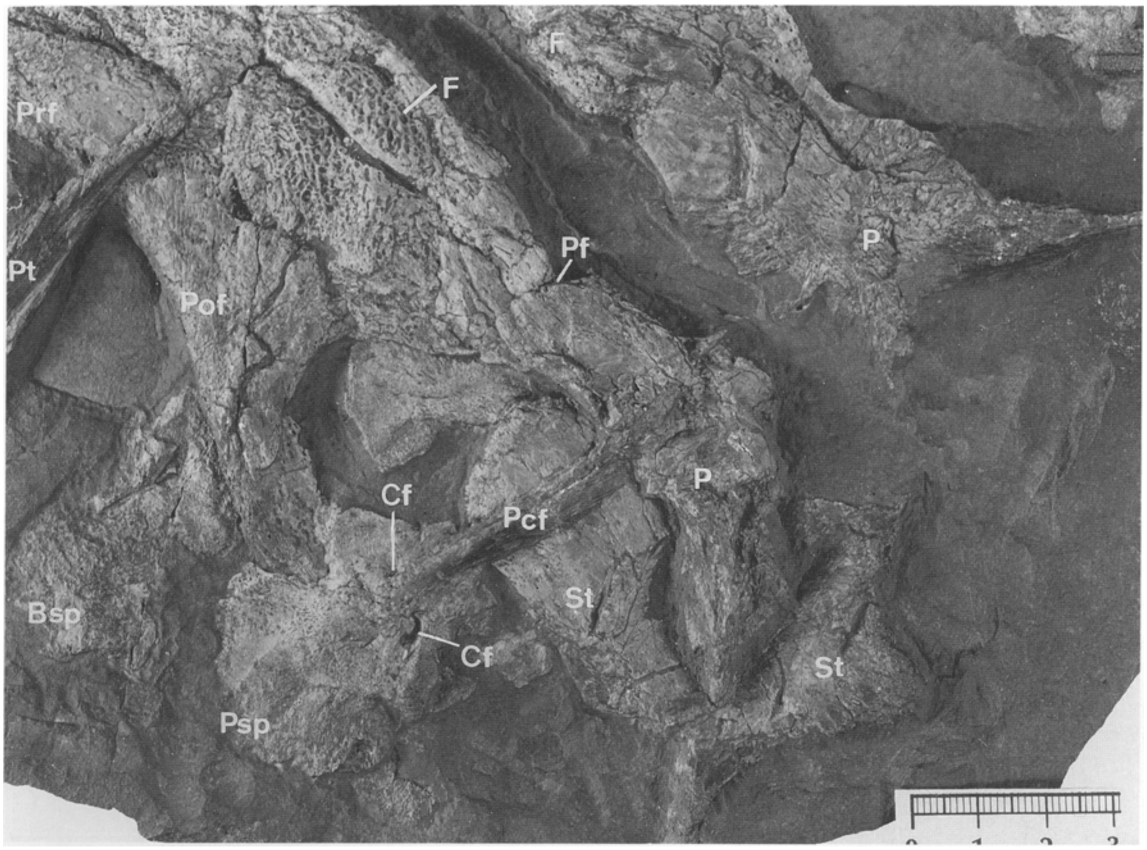

Fig. 6. *Mikadocephalus gracilirostris* n. gen., n. sp.- Holotype (GPIT 1793/1). Parasphenoid with the processus cultriformis and the two foramen arteria carotici interna posterius; the parasphenoid is not coossified with the basisphenoid. Foto: GERBER (Tübingen).- For abbreviations see text.- One unit of the scale bar: 10 mm.

broad element found in the other Triassic taxa, which leaves little room for the interpterygoid vacuities. In this regard the new specimen is definitely as advanced as any Jurassic ichthyosaur. Another probably advanced feature is the lack of posteromedial pterygoid processes found in other Triassic forms, e.g. *Mixosaurus* (VON HUENE 1916). Another incomplete bone preserved as an isolated element represents the anterior portion of the right pterygoid exposed in dorsal view.

Parasphenoid: The parasphenoid (Fig.6) is very well preserved. It is exposed in ventral view. Much of the processus cultriformis (Fig.6) is lost and what remains has been in part squashed upon the underlying bones of the skull roof. The basal plate is, however, quite well preserved. It is of roughly rectangular shape. Its posterior margin is notched medially. The lateral margins are of complex shape, being laterally convex posterior to basipterygoid process, showing a distinct notch on the left posterolateral corner, which is present - albeit smaller and less clearly defined, which is probably due to differential deformation - on the right side as well (Fig.6). Behind the well developed basipterygoid processes, the bone is markedly constricted. The ventral surface is somewhat bulging from the centre forwards, this medial bulge becoming continuously more pronounced anteriorly and uninterruptedly merging with the cultriform process. The same ridge of the parasphenoid can be observed in *Temnodontosaurus platyodon* (GODEFROIT 1992) and *T. trigonodon* (VON HUENE 1931, pers. obs.), but is not present in other Jurassic ichthyosaurs.

There is a well developed basipterygoid process forming a clear articulation facet (Fig.6), indicating that some movement might have been possible at the basicranial joint. The internal carotid arteries (Fig.6) enter the parasphenoid ventrally via small paired foramina, the left of which is very well visible, whereas the right one is slightly occluded by deformation. These are situated lateral to the posterior extending central ridge. In most post-Triassic ichthyosaurs and in *Mixosaurus* amongst Triassic forms (WIMAN 1912; VON HUENE 1916; pers. obs.) there is only one large foramen piercing the parasphenoid and/or basisphenoid medially. In *Temnodontosaurus*, however, there are always two carotidal foramina separated by the posterior extension of the cultriform process (FRAAS 1913; VON HUENE 1931; GODEFROIT 1992; pers. obs.). The same appears to be the case in *Shastasaurus neoscapularis* (MC GOWAN 1994) judging from MC GOWAN's figure (the feature is not explicitly described). There are two additional much smaller foramina directly posterior to the foramen arteria carotici interna posterius. They have not yet been observed in any other ichthyosaur and their function remains obscure.

The cultriform process is slender and narrow, being clearly offset from the basal plate. It does not bear a pronounced ventral ridge as it does in *Temnodontosaurus* (pers. obs.).

A remarkable feature of the parasphenoid is that the bone was probably relatively thin, as evidenced by the considerable deformation it has undergone. This is in strong contrast to the massive basisphenoid ossifications of post-Triassic ichthyosaurs and might be a further corroboration of the interpretation presented below concerning the basisphenoid.

Elements of the chondrocranium

? Basisphenoid: The parasphenoid (Fig.6) and basisphenoid (Fig.6) are completely coossified in all Jurassic ichthyosaurs in which this feature is known. A small, irregularly shaped bone, lying adjacent to the complete parasphenoid could, however, represent a separately ossified basisphenoid. It shows a very cancellous surface (Fig.6), as most of the other enchondral bones of the specimen. It does not appear to be severely damaged, and its grossly triangular shape with a narrow anterior extension and two lateral flanges (Fig.6) reminds of the general outline of the basal plate of the parasphenoid, being distinctly smaller, however. If this element really represents the basisphenoid, it is most probably seen in ventral view. Since it is almost complete and of such unusual shape, there appear no other possible interpretations for this ossification at the moment.

Epipterygoid: One of the most interesting features of the specimen is the first record of an epipterygoid (Fig.5) in an Triassic ichthyosaur. It is preserved in natural position with the left pterygoid (Fig.5). As in *Ichthyosaurus* (Mc Gowan 1973) it is situated right anterior to the lamina ascendens. Ventrally it is fanning out forming an expanded "footplate", sending off a very slender and gracile ascending process dorsally, which is broken and incompletely preserved (Fig.5). The parts of the footplate situated anterior and posterior to the origin of the ascending process are subequal in size. The epipterygoid is squashed completely onto the dorsal surface of the pterygoid and it is clearly visible that it was a very thin and fragile ossification, which largely accounts for its rare preservation in ichthyosaur skulls in general.

Quadrate: The right quadrate (Fig.7) is nearly completely preserved and is exposed in anterior view. It is a large, broad, almost ear-shaped bone with a thick and massive ventral condyle (Fig.7) for the articulation with the mandible. Above the condyle, the bone forms a flat ascending plate (Fig.7), which becomes thinner from below upwards. Laterodorsal to the articular condyle, the bone narrows, its medial margin being concave, forming an almost perfect semicircle. At the medioventral edge of the quadrate there is a small triangular projection (Fig.7), which has not been described in any other ichthyosaur. Its functional importance – if any – remains obscure. Between the condyle and the triangular projection another small medioventral process can be seen. Above the massive ventral condyle there is a clear facet for the processus quadratus of the quadratojugal (Fig.7). The left quadrate (Fig.5) is also exposed in anterior view, but its laterodorsal part is heavily damaged. The small triangular projection and the facet for the processus quadratus of the quadratojugal can also be seen on the left quadrate.

Supraoccipital: The small, poorly preserved supraoccipital is exposed in posterior view. It is a massively built, arched bone. Its ventral margin forms the dorsal margin of the foramen magnum. Lateral to the foramen magnum small facets for the two exoccipitals can be seen on the ventral edge. At the left dorsolateral margin there is a depression, which might represent a large foramen similar to those described in *Ophthalmosaurus* and *Ichthyosaurus* (Andrews 1910; Mc Gowan 1973; pers. obs.). The right dorsolateral margin is compressed so that no foramen is visible.

Additional features of the cranial skeleton

Dentition: Only part of the upper jaw dentition is preserved. The teeth of the premaxilla are relatively small and only few of them are preserved. They are conical, pointed and straight with a very slender tip, and bear fine parallel striations on the surface of the crown. The teeth from the anterior part of the maxilla (Fig.3) are somewhat larger, but otherwise similar to the premaxillary teeth, except that the bases of the maxillary tooth crowns are somewhat broader and the striations on the surface are deeper. The most posterior maxillary tooth crowns broaden considerably and their tips are somewhat rounded (Fig.3). No carinae can be seen on any of the teeth.

Sclerotic plates: Only four very thin and flat plates of the sclerotic ring are preserved. Two of these are preserved in natural articulation, showing a complex sutural association. They are exposed from the external side. The internal portion of the lateral surface is extremely well preserved but the external portion, which is normally flexed, as described in *Ichthyosaurus* (Mc Gowan 1973) and *Stenopterygius* (Mazin 1986), is strongly broken and flattened. The other two sclerotic plates are heavily damaged.

? Stapes: There is only one bone which could be interpreted as a stapes. It is very flattened and not as thick as described for *Ophthalmosaurus* (Andrews 1910) or *Ichthyosaurus* (Mc Gowan 1973). It is club-shaped, with a broader proximal end, which probably contacted the basioccipital as is usual in ichthyosaurs. The more slender distal end probably contacted the quadrate. The surface of the element is very rough and granular.

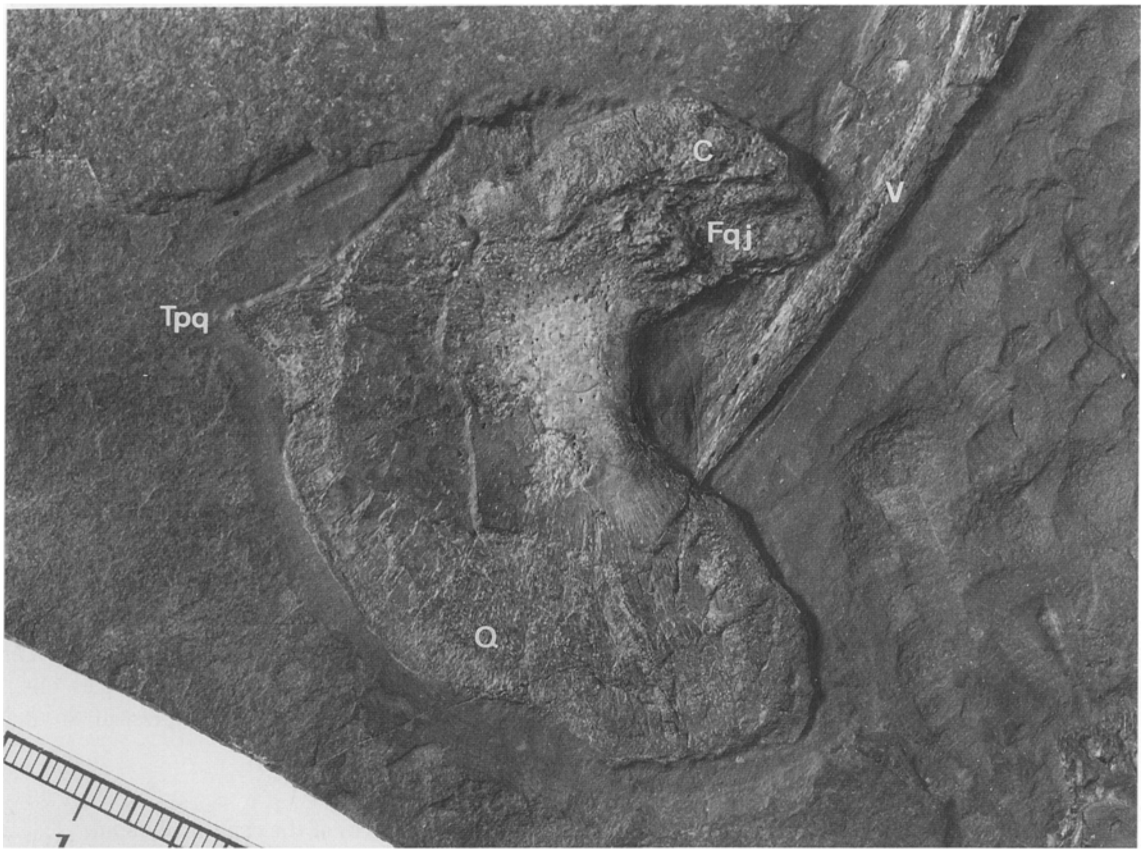

Fig. 7. *Mikadocephalus gracilirostris* n. gen., n. sp.- Holotype (GPIT 1793/1). Right quadrate in anterior view with the triangular medioventral process. Foto: GERBER (Tübingen).– For abbreviations see text.– One unit of the scale bar: 10 mm.

Elements of the lower jaw

Splenial: Only the right splenial is preserved and is exposed in medial view. The thinner anterior half of the bone is well preserved, but the thicker posterior half shows many breaks and has been pressed onto several other bones (Fig.5) so that no further information can be obtained. The anterior end of the bone, which contacted the dentary, is divided into a longer, thicker ventral, and a shorter, less robust dorsal process. The ventral process shows a slightly curved, concave facet for the dentary, as is also described in e.g. *Ophthalmosaurus* (ANDREWS 1910) and *Ichthyosaurus* (SOLLAS 1916). The preserved posteroventral part of the splenial shows a slightly curved facet, probably for the angular. There is a long and slender depression in the middle of the splenial (Fig.5), between the dorsal and the ventral margins of the bone, forming the medial border of the canalis meckelii (SOLLAS 1916).

Angular: Only the posterior region of the left angular (Fig.5), which is exposed in internal view, can be positively identified. It shows a considerable dorsal expansion giving it an almost oval shape. At the ventral margin of the angular the nearly three-dimensionally preserved facet for the surangular (Fig.5) can be seen to be similar to e.g. *Ichthyosaurus* (SOLLAS 1916). Nearby the right splenial a slender bone is found, which might be interpreted as the anterior part of the right angular.

Prearticular: The right prearticular is well preserved, probably in internal view. The anterior end of the bone is, however, lost. This is also the case in the left prearticular, which equally shows its internal aspect. The prearticular is a thin, slender, crescent-shaped element with a concave dorsal and convex ventral margin. Ventrally there is a posterior longitudinal facet for the articular and a medial facet for the angular. In this region the surface has a rather coarse texture.

Coronoid: Two very small, long and slender bones are preserved close to the rest of the lower jaw. One is quite well preserved, and the best interpretation for such an extremely thin, slender and straight bone is the coronoid as described in *Leptopterygius nuertingensis* (VON HUENE 1931) and *Ichthyosaurus* (MC GOWAN 1973).

Surangular: Both surangulars are preserved in natural articulation (Fig.5) with the articulars, and a serrate suture can be seen between them, which is in contrast to the situation in post-Triassic ichthyosaurs where a firm suture between these bones is never established. Both surangulars are exposed in internal view. The left surangular is well preserved in the posterior and anterior region, but in the middle it is heavily damaged and no further information can be obtained. The right surangular is rather well preserved, but the anterior third of the bone is damaged. The surangular is a very long bone with a slender anterior part and a thin elongation that broadens posteriorly and becomes thickened in the region of the processus coronoideus (Fig.5), as in e.g. *Ichthyosaurus* (SOLLAS 1916) or *Shonisaurus* (CAMP 1980). Anteriorly of the processus coronoideus two foramina are visible (Fig.5). The posterior foramen has only half the size of the big anterior one, which has a diameter of at least 6 mm. At the ventral margin of both surangulars, the facet for the angular can be identified. Posterodorsally, immediately in front of the articular there is an unusually large, rounded and roughened processus coronoideus. In the middle region of the right surangular the facet for the prearticular is preserved and in the anterior part of the left surangular the facet for the dentary is visible.

Articular: Both articulars are excellently preserved in natural position, at the posterior ends of the surangulars. They have an intimate sutural contact with the surangulars (Fig.5), and this is probably the reason for the unusual preservation in natural articulation. The posterior position of the articular indicates that the retroarticular portion of the mandible was unusually short. They are rather small bones exposed in internal view. The surface of the articular is quite different from the other bones of the lower jaw, being rather rough and granular. The articular is almost square (Fig.5), with a slightly concave medial surface, as in e.g. *Ophthalmosaurus* (ANDREWS 1910) and *Ichthyosaurus* (MC GOWAN 1973). The prearticular facet is preserved only in the right articular.

Discussion

Most of the described Triassic ichthyosaur taxa are only known from rather inadequate material, as far as the head skeleton is concerned. The holotype specimen of *Mikadocephalus gracilirostris* is unusual in that it yields a wealth of data on cranial osteology, but shows nothing of the postcranial skeleton. Comparison is thus restricted to those species, which are known from comparatively good skull material. This excludes the following genera from closer comparison: *Californosaurus* KUHN (= *Delphinosaurus* MERRIAM), *Himalayasaurus* DONG (in YOUNG & DONG), *Hudsonelpidia* MC GOWAN, *Merriama* BOULENGER (= *Leptocheirus* MERRIAM), *Omphalosaurus* MERRIAM, *Pachygonosaurus* VON HUENE, *Pessosaurus* WIMAN, *Svalbardosaurus* MAZIN, *Tholodus* VON MEYER, *Tibetosaurus* YOUNG et al. and *Chaohusaurus* DONG (in YOUNG & DONG).

More or less reliable and adequate cranial information can be gained only on the following genera: *Cymbospondylus* LEIDY, *Grippia* WIMAN, *Mixosaurus* BAUR, *Phalarodon* MERRIAM, *Shastasaurus* MERRIAM, *Shonisaurus* CAMP, *Parvinatator* NICHOLLS & BRINKMAN and *Thaisaurus* MAZIN et al. Comparison will thus concentrate on these forms, the others are treated in a final short section.

Mixosaurus cornalianus (BASSANI 1886)

This is the best known and most common ichthyosaur from Besano and the Grenzbitumenzone-Beds of Monte San Giorgio. The GPIT possesses a very good collection of partly excellently preserved and prepared material of this small ichthyosaur, which allowed direct comparisons to be made. It is thus possible to supplement the short and incomplete existing descriptions of the cranial morphology given by REPOSSI (1902) and VON HUENE (1916, 1925, 1936, 1949) by personal observations.

Mixosaurus cornalianus differs from *Mikadocephalus* firstly by its much smaller size, never reaching a skull length of much more than 20 cm. The size range of this species is well known, because several hundred specimens have been discovered, including clearly mature animals (BRINKMANN 1996). Apart from size, there are numerous morphological features, which distinguish the two taxa. In *Mixosaurus cornalianus* the posterior maxillary teeth are generally more blunt and shorter than the rest of the dentition, and the upper tooth row extends beyond the level of the dorsal maxillary process. The posteriormost teeth of *Mikadocephalus* are also somewhat shorter and broader, but they are not blunt. The orbit is relatively much larger, the postorbital skull much shorter in *Mixosaurus cornalianus*. The dorsal temporal opening is present only as a small slit-like aperture. It is bordered by the supratemporal and parietal only (VON HUENE 1949; pers. obs.; contra CALDWELL 1996), whereas it is bordered by the postfrontal, supratemporal and parietal in *Mikadocephalus* in the usual way. The frontals of *Mixosaurus cornalianus* are very large elements, whereas the nasals are very short, not reaching beyond the level of the anterior orbital margin, the quadratojugal lacks a distinctly offset processus quadratus sitting on a constricted "collar" of bone, being more similar to forms such as *Stenopterygius* (pers. obs.), the pterygoids are very wide, the interpterygoid vacuities practically non-existing, and the pterygoids bear well developed posteromedial processes. The foramen arteria carotici interna posterius is unpaired in *M. cornalianus* (WIMAN 1912). The structure of the temporal region of *Mixosaurus cornalianus* will be discussed elsewhere (MAISCH, SCHOCH & MATZKE, in prep). At any rate the differences cited above show, that this taxon is not only specifically but also generically distinct from *Mikadocephalus gracilirostris*.

Mixosaurus atavus (QUENSTEDT 1852)

This taxon is mainly known from an incomplete skull from the Lower Muschelkalk of South Western Germany described in detail by VON HUENE (1916). It is similar to *Mixosaurus cornalianus*, and the differences distinguishing that species from *Mikadocephalus* equally apply to *Mixosaurus atavus*. The orbits are somewhat smaller, the postorbital skull segment lower and the temporal fenestrae larger than in *Mixosaurus cornalianus.* In these characters *Mixosaurus atavus* approaches the conditions seen in *Mikadocephalus* a little closer than *Mixosaurus cornalianus* does, but otherwise the two taxa are also different in almost every respect of cranial osteology and can safely be regarded as generically distinct.

Phalarodon fraasi MERRIAM 1910

Only one incomplete skull of this interesting, small, durophagous ichthyosaur from the Middle Triassic of Nevada is known. It was described in detail by MERRIAM (1910) and VON HUENE (1916). Most of the snout and the postorbital skull segment are missing. What remains of the skull is generally similar in proportions and structure to *Mixosaurus*, especially the large size of the frontals and the small posterior extension of the nasal bones. The most noteworthy features of *Phalarodon fraasi* are its large, flattened maxillary and posterior dentary teeth, which constitute a device for crushing shells and resemble the palatal teeth of placodonts in form and probable function. There are two maxillary tooth rows. It is evident from the structure of both the skull roof and the dentition, that *Phalarodon fraasi* is very distantly related at best to *Mikadocephalus.* Furthermore it is a much smaller animal, as far this can be ascertained.

Mixosaurus (?) *nordenskjoeldi* (HULKE 1873)

This species, usually referred to as a species of *Mixosaurus*, but much closer in its dental characters to *Phalarodon fraasi* (MERRIAM 1910), is known from the Middle Triassic of Spitzbergen. Only sparse material of the cranial skeleton has been described by WIMAN (1910) and was further discussed by VON HUENE (1916) and MAZIN (1984). The picture that emerges is that of another small, heterodontous ichthyosaur with crushing teeth at least in the posterior part of its jaws. It is surely very different from *Mikadocephalus.*

Thaisaurus chonglakmanii (MAZIN et al. 1991)

This small presumably lower Triassic ichthyosaur from Thailand is a very small species, in contrast to *Mikadocephalus.* The only known specimen is badly preserved and incompletely described. It differs from *Mikadocephalus* in its dentition, which is totally isodontous, as well as in the postfrontals not reaching the margin of the temporal fenestra, which is a unique condition in ichthyosaurs. There are, however, some resemblances, such as the small exposure of the frontals on the skull roof, the position of the parietal foramen and the general proportions of the skull, *Thaisaurus* also being a very tenuirostrine animal with a rather long postorbital skull region. More material is needed, however, before any phylogenetic conclusion might be drawn from these characters.

Shonisaurus popularis CAMP 1976

Although known from numerous specimens, the skull structure of this most gigantic Triassic ichthyosaur from the upper Triassic of Nevada is very incompletely known and therefore a comparison is difficult. The snout of *Shonisaurus* is very long, but proportionally much more robust than in *Mikadocephalus.* The dentition shows definite signs of reduction, especially in the posterior part of the jaws. The premaxilla apparently possesses a posterodorsal extension, the maxilla is very short anteriorly and lacks a dorsal postnarial process. The parietals form a high sagittal crest, as in *Cymbospondylus petrinus.* The structure of the temporal and postorbital regions are very difficult to assess from CAMP's (1980) description and reconstruction. The differences cited above, however, already clearly indicate that there is no similarity between *Shonisaurus* and *Mikadocephalus.*

Shastasaurus alexandrae MERRIAM 1902

This species from the upper Triassic of California is known from a very well preserved, but incomplete skull lacking most of the snout, described by MERRIAM (1902) and VON HUENE (1916). It is not dissimilar in proportions and shape from that of *Mikadocephalus.* The main difference is that the frontals in *Shastasaurus alexandrae* form much of the margin of the large temporal fenestrae and that the pterygoids are almost as wide as in *Mixosaurus*, equally possessing posteromedial processes, the interpterygoid vacuities being small.

A strong similarity is the large posterior extension of the nasals, which reach backwards to at least the middle of the orbits. *Shastasaurus alexandrae* and *Mikadocephalus* are much more similar to each other than either is to any of the known 'mixosaurids' (*Mixosaurus, Phalarodon*). The differences in configuration and size of the frontals and pterygoids alone are considered more than sufficient to keep the two taxa apart generically.

Shastasaurus altispinus MERRIAM 1902

Most of what is known about the skull of this species is based on fragments recently described from the Middle Triassic of Mexico by CALLAWAY & MASSARE (1989b) and referred to this originally Californian species. The validity of *Shastasaurus altispinus* has recently been questioned by MC GOWAN (1994). The snout of *Shastasaurus altispinus* shows a dentition made up of large pointed, conical and carinate teeth, set in distinct alveoli. It shows the typical configuration of the shastasaurid premaxilla with a long posterodorsal spur bordering most of the dorsal narial margin. It should be noted in this context, that a posterodorsal extension of the premaxilla is also a general feature of all post-Triassic ichthyosaurs, though not as pronounced as in the shastasaurids. It is absent in all other adequately known Triassic taxa; *Shastasaurus altispinus* is clearly generically distinct from *Mikadocephalus.* Because practically nothing is known about the posterior portion of the skull in *Shastasaurus altispinus* and the snout is missing in *Shastasaurus alexandrae*, it is practically impossible to assess the synonymy of these two species.

Shastasaurus neoscapularis Mc Gowan 1994

This is one of the best known Triassic ichthyosaurs. Although there is only a single known specimen from the Lower Norian of British Columbia, it includes an almost complete skull. Comparison is limited by the rather brief existing description and the incomplete preservation of the skull of *Shastasaurus neoscapularis.* The overall shape and proportions of the skull are quite similar in the two taxa, as is the dentition, which consists of numerous small conical, pointed teeth.

One noteworthy feature of *Shastasaurus neoscapularis* clearly seen in Mc Gowan's (1994) figure 3 is the structure of the basisphenoid, which is a more or less quadrangular plate with two large openings for the carotid arteries separated by a ridge. This morphology is very reminiscent of the Lower Jurassic *Temnodontosaurus trigonodon* (pers. obs.) and *T. platyodon* (Godefroit 1992), very different to *Mikadocephalus*, where the carotidal foramina are small, slit-like openings. Because the morphology of the basisphenoid is a very constant feature in Lower Jurassic ichthyosaurs, being diagnostic at the generic level (pers. obs.), this feature alone is sufficient to support the generic distinctiveness of *Mikadocephalus* from *Shastasaurus neoscapularis.* Further differences lie in the apparently much shorter postorbital region of *Shastasaurus neoscapularis*, the shape of the maxilla with a short pointed anterior extension, the shape of the premaxilla, which shows a distinctive supranarial spur, and the primitive feature of the parietal foramen being entirely enclosed within the parietals. The occurrence of this latter feature in such an otherwise highly derived Triassic ichthyosaur creates problems for Mazin's (1982b) hypothesis that, on the basis of the position of the parietal foramen within the paritals, *Grippia longirostris* is the most primitive ichthyosaur.

Cymbospondylus petrinus Leidy 1868

This is apart from *Mikadocephalus*, the best known of all Triassic ichthyosaurs, at least concerning the structure of the skull, which has been described and figured by Merriam (1908), von Huene (1916), Camp (1980), Sander (1989) and Massare & Callaway (1990). Although the available description are contradictory to some extent, it is clear that *Cymbospondylus petrinus* is very different to *Mikadocephalus* in several important features. For example the snout is somewhat shorter and the rostrum much more robust, the orbit is distinctly smaller, the temporal fenestrae larger, the maxilla is taller and has a shorter postnarial process, the premaxilla has a long and slender supranarial spur, the jugal shows a posteroventral flange, the frontals are very large and enter the anterior temporal margin, while the nasals apparently have long posterolateral processes reaching either the supratemporal or the squamosal, the postfrontals are large elements with a considerable posterior extension, the parietals form a sharp and narrow sagittal crest, the supratemporal lacks a large posteroventral flange, the pterygoids are broad and of the *Shastasaurus* type. Similarities are encountered in the considerable extent of the nasals onto the dorsal skull roof, the shape of the quadratojugal, the long postorbital skull region, the shape of the lacrimal and the reduction of the maxillary dentition. *Cymbospondylus petrinus* is a very large ichthyosaur, the largest specimen known being more than twice the size of *Mikadocephalus.*

Cymbospondylus buchseri Sander 1989

This species is of particular interest, since it is the only other large ichthyosaur described from the Grenzbitumenzone Beds of Monte San Giorgio. In its skull proportions and size it is somewhat closer to *Mikadocephalus* than *Cymbospondylus petrinus.* It is, however, also different in many respects, especially the structure of the temporal and cheek region. The quadratojugal is unfortunately not known in *Cymbospondylus buchseri.* The nasal and supratemporal, and the prefrontal and supratemporal, establish contact (Sander 1989). The postfrontal is larger and extends further posteriorly than in *Mikadocephalus.* The frontals are large and contribute to the anterior margin of the temporal fenestra. The snout is much more robust and less clearly demarcated from the rest of the skull as it is in *Mikadocephalus.*

Grippia longirostris Wiman 1928

This is surely the most enigmatic and discussed of all Triassic ichthyosaurs. This probably largely results from the incomplete preservation of the known material and the large variance encountered in the existing descriptions and illustrations of the holotype skull, which was destroyed with part of the Hamburg collection in World War II. *Grippia* is a small animal and despite its specific name, a very short-snouted ichthyosaur (Wiman originally thought that the strange animal belonged to a new order of reptiles and considered the long snout to be a remarkable character). The nasals are very short. The dentition shows a considerable amount of heterodonty. There are two maxillary tooth rows and the palatines are also toothed. There has been much made of the temporal region of this taxon because of the presence of a supratemporal, even though this is in fact a feature of all ichthyosaurs and not a primitive trait restricted to *Grippia longirostris.* What is much more interesting about the temporal region of this taxon is the apparent fusion of squamosal and quadratojugal, which is definitely not present in *Mikadocephalus* or probably all other Triassic ichthyosaurs. It was, however, contradicted by von Huene (1943), the last to study the holotype skull. Generally *Grippia longirostris* is extremely dissimilar to *Mikadocephalus.*

Parvinatator wapitiensis NICHOLLS & BRINKMAN 1995

This ichthyosaur from the Lower Triassic Sulphur Mountain Formation of British Columbia is clearly distinguishable from *Mikadocephalus* by its much smaller size. It furthermore differs in its dentition, where the largest teeth are found in the premaxilla, whereas the maxillary teeth are smaller and more pointed. The situation is vice versa in *Mikadocephalus*. The number of maxillary teeth is about half that in *Mikadocephalus* (10 vs. > 20).The morphology of the mandible in *Parvinatator* is unique among all known ichthyosaurs, with the surangular being extremely high and a well developed hook-like retroarticular process being present. It is thus clear that *Parvinatator* and *Mikadocephalus* are generically different and not closely related. Some comment is necessary on the homologies of the temporal bones in ichthyosaurs proposed by NICHOLLS & BRINKMAN (1995). There is not the least evidence that the quadratojugal was lost in any known ichthyosaur. The element labelled as squamosal by NICHOLLS & BRINKMAN (1995) is the quadratojugal, which is very similar in shape and relationships to the surrounding bones to e.g. *Ichthyosaurus* (MC GOWAN 1973). NICHOLLS & BRINKMAN correctly point out that three bones are present in the temporal region of *Mixosaurus* and that the uppermost element of the ichthyosaurian cheek is not the squamosal but an unusually large supratemporal. The situation seen in *Mixosaurus* is, however, not restricted to that particular genus but found in the large majority of post-Triassic ichthyosaurs as well (GODEFROIT 1994; MAISCH & HUNGERBÜHLER, in press; MAISCH in press).

Of the remaining Triassic taxa *Omphalosaurus* MERRIAM, which is represented by the type species *O. nevadanus* MERRIAM and *O. nettarhynchus* MAZIN & BUCHER in North America, several inadequately known species (which might all be synonymous) namely *O. nisseri* (WIMAN), *O. arcticus* (WIMAN) and *O. pinquis* (WIMAN) from Spitzbergen and the newly discovered *O. wolfi* TICHY from Central Europe, is not known from complete and well preserved cranial material. The skull is best preserved in the type species. It was described on several occasions by MERRIAM (1906), MERRIAM & BRYANT (1911), VON HUENE (1922) and most recently MAZIN (1986). The picture emerging is that of a very aberrant and specialised -surely not "primitive"- ichthyosaur with a very short-snouted and heavily built skull and several rows of blunt crushing teeth in both upper and lower jaw. It is clearly very different to *Mikadocephalus*.

Tholodus schmidi VON MEYER 1851 from the German Muschelkalk, long thought to represent an actinopterygian fish, is only known from isolated teeth and jaw fragments, which most closely resemble the crushing dentition of *Omphalosaurus* among other known ichthyosaurs. There is no resemblance to the dentition of *Mikadocephalus*.

Merriama zitteli (MERRIAM 1903) from the upper Triassic of California is known from a well preserved, but unfortunately very incomplete skull described in detail by MERRIAM (1903, 1908). It resembles *Mikadocephalus* in the possession of large eyes and a slender and strongly curved jugal, as well as in the shape and mutual relationships of lacrimal and maxilla. As far as it can be ascertained, the dentition approaches the aulacodont pattern with no distinct alveoli being formed, which is at least partially in contrast to *Mikadocephalus*. It is thus evident that, even though the differences in the dentition allow generic separation, there is a definite possibility that *Mikadocephalus* and *Merriama zitteli* are quite closely related. Too little is, however, known about the latter taxon to allow a definite decision on this point.

Svalbardosaurus crassidens MAZIN 1981 from the middle Triassic of Spitzbergen is an inadequately known species based on a fragment of an unidentified dentigerous bone with three presumably ichthyosaurian teeth of very large size, which do not appear to be set in distinct alveoli. The ichthyosaurian nature of this specimen is in our opinion unsubstantiated. They could as well be teeth of an unknown large actinopterygian fish or labyrinthodont amphibian, two groups which are very common in the Lower Triassic of Spitzbergen. They do not show any distinctive ichthyosaurian features. *Svalbardosaurus crassidens* MAZIN 1981 should thus be considered a nomen dubium. The teeth do not resemble the dentition of *Mikadocephalus*.

Hudsonelpidia brevirostris MC GOWAN 1995 from the Norian of Canada is one of the better known Triassic taxa. The skull of the only known specimen is, however, unfortunately very badly preserved. It is a small and short-snouted animal with a very large orbit and several foramina piercing the anterior part of the snout, which are unknown in any other ichthyosaur. The dentition appears to be reduced. The total absence of teeth is perhaps not readily explicable by the weathering of the specimen, as proposed by MC GOWAN (1995), since all the snout bones appear to be preserved in a still recognizable condition. *Hudsonelpidia* is clearly distinct from *Mikadocephalus*.

Pessosaurus polaris (HULKE 1873) is a large ichthyosaur from the middle Triassic of Spitzbergen of which only some skull fragments are known, apart from postcranial material. *Pessosaurus suevicus* VON HUENE 1916, a smaller species from the German Muschelkalk, is only known from isolated vertebrae. The jaws of *Pessosaurus* apparently show typically aulacodont tooth implantation (MAZIN 1983). The morphology of this genus is still very inadequately known. Its thoracic vertebrae are, however, very distinctive and easily identifiable (WIMAN 1910; VON HUENE 1916), and it is a valid taxon.

Utatsusaurus hataii SHIKAMA, KAMEI & MURATA 1978 from the Spathian of Japan is known from a number of specimens. Good skull material is, however, not preserved. The dentition is aulacodont and consists of very small, more or less pointed teeth (MOTANI 1996), the orbits are large, and the snout is relatively long and slender. The latter two features are reminiscent of *Mikadocephalus*, but are found in many ichthyosaurs, not pointing to any close relationship. The dentition is so different as to prove the generic distinction between the two, as well as the great size discrepancy and stratigraphic gap.

Chaohusaurus geishanensis YOUNG & DONG 1972 is apparently known from a fairly good skeleton retaining most of its skull from the Spathian of China. The existing description does not allow detailed comparisons to be made. The snout is very short and robust, resembling *Grippia longirostris* rather than *Utatsusaurus hataii*. There is some heterodonty in the dentition.These are features also found in both *Grippia* and *Mikadocephalus*. The frontals are apparently excluded from the temporal margin and the parietal foramen is largely contained within the parietals as is also the case in both *Grippia* and *Mikadocephalus*. These features are probably largely plesiomorphies. Skull shape in *Chaohusaurus geishanensis* does not resemble that in *Mikadocephalus*.

Chensaurus MAZIN et al. 1991 represented by the two species *C. chaoxianensis* (CHEN 1985) and *C. faciles* (CHEN 1985) from the Lower Triassic of China, is inadequately known, even though quite good material is available. It is a short-snouted form with a skull resembling that of *Grippia* in overall shape.

Himalayasaurus tibetensis DONG 1972 (in YOUNG & DONG 1972) from the Norian of Tibet is very incompletely known. The snout fragment described by DONG (in YOUNG & DONG 1972) shows that the animal possessed a very robust rostrum of probably only medium length, closely resembling *Cymbospondylus*. The premaxilla apparently extends posterodorsally to take part in the formation of the dorsal narial margin, as in *Cymbospondylus petrinus* and *Shastasaurus altispinus*, but in contrast to *Mikadocephalus*. The teeth are implanted in distinct alveoli throughout the jaws, being laterally compressed and showing anterior and posterior carinae, as in *Shastasaurus altispinus*. These features clearly distinguish *Himalayasaurus tibetensis* from *Mikadocephalus*, but show it to be probably closely related to *Shastasaurus*.

Tibetosaurus tingjiensis YOUNG et al. 1982 from the Norian of Tibet is essentially only known from isolated scraps. The teeth referred to this form indicate shastasaurid affinities. The species is much larger than *Mikadocephalus* and the teeth are more robust.

No skull is known in either *Toretocnemus californicus* MERRIAM 1903 or *Californosaurus perrini* (MERRIAM 1902), both from the Carnian of California, or *Pachygonosaurus* VON HUENE 1916 from the Polish Muschelkalk. The latter genus was erected on the basis of isolated vertebrae, the morphology of which is very distinctive. The thickened rib articulations and the small diameter of the central depression of the articulatory surface are not found in the dorsal vertebrae of other Triassic ichthyosaurs. In contrast to CALLAWAY & MASSARE (1989a) we consider the taxon to be valid, but only include the vertebrae described by VON HUENE (1916) from the Muschelkalk of Poland. No specific name was ever proposed for *Pachygonosaurus*. We therefore propose the name *Pachygonosaurus robustus* n. sp. The holotype is the dorsal vertebral centrum illustrated by VON HUENE (1916: 39, fig. 69) from the Upper Muschelkalk (Rybnaer Kalk) of Gorny Slask, Poland, preserved in the Museum für Naturkunde der Humboldt-Universität, Berlin. It is possible that these vertebrae belong to *Tholodus schmidi*. Their morphology suggests pachyostosis of the ribs, expectable in a highly derived omphalosaurid such as *Tholodus*. Before this can be demonstrated, both taxa must be allowed to stand.

In consequence, the specimen described above can clearly not be identified with any hithero described genus of Triassic ichthyosaur and its interpretation as a new genus and species – *Mikadocephalus gracilirostris* – is thus justified.

The phylogenetic position of *Mikadocephalus gracilirostris*

Mikadocephalus retains a number of characters, which can possibly be regarded as plesiomorphic within the Ichthyosauria. These are:

- A slight heterodonty of the upper and lower dentition, also found in *Grippia*, *Mixosaurus* and *Chaohusaurus*, but not in *Utatsusaurus* or *Thaisaurus*.
- The presence of a well developed postnarial process of the maxilla that excludes the lacrimal from the external narial opening, present in all adequately known Triassic ichthyosaurs with the probable exception of *Ichthyosaurus janiceps* (MC GOWAN 1996) and *Grippia longirostris* (VON HUENE 1943).
- The anterior maxillary teeth, at least, are set in distinct alveoli (the aulacodont tooth-implantation of *Utatsusaurus hataii* recently demonstrated by MOTANI (1996) does, however, raise again the question what kind of tooth-implantation must be considered plesiomorphic for the Ichthyosauria).

Mikadocephalus is, however, advanced with respect to the ground plan of ichthyosaurs -assumed to be most closely represented at present by *Mixosaurus*, at least concerning the skull- in the following characters:

- The premaxilla has at least a small supranarial process, as in all Jurassic forms, which contrasts with the condition in *Mixosaurus* (VON HUENE 1949; pers. obs.).
- The nasals are very large and reach posteriorly to the level of the middle of the orbit, which contrasts with the situation in *Mixosaurus* (VON HUENE 1949; pers. obs.) and *Grippia* (MAZIN 1982b).
- The frontals are excluded from the margins of the temporal fenestra and do form only a small portion of the skull roof. This character is surely advanced, since in *Mixosaurus* (VON HUENE 1949; pers. obs.) and probably *Grippia* (MAZIN 1982b) the frontals are large bones. A contact of the frontal with the anterior margin of the temporal fenestra is found in a number of Triassic taxa, such as the shastasaurids, and it might thus be a primitive trait. The situation in *Mixosaurus* is, as indicated above, not comparable to that in any other ichthyosaur since this taxon lacks well developed temporal fenestrae.
- The temporal openings are larger than 1/3 the size of the orbita. They resemble all other "normal" ichthyosaurs, being fundamentally different from the small slit-like aperture found in *Mixosaurus* (VON HUENE 1936, 1949; pers. obs.).
- The teeth do show an aulacodont mode of implantation at least in the posterior portion of the maxilla (but see discussion above).
- The carotidal foramina are paired, whereas they are unpaired in *Mixosaurus* (VON HUENE 1916; WIMAN 1912; pers. obs.).
- The quadrate process of the quadratojugal is long, the facet

for contact with the quadrate being clearly set off from the main body of the bone, being situated on a distinct "collar". This is reminiscent of the situation in *Cymbospondylus* (Merriam 1908). The quadrate process in *Mixosaurus* is - in contrast - very short and inconspicuous (pers. obs.). There is a possibility that this condition in *Mixosaurus* is directly correlated to the shortening of the postorbital skull region that has occured in this genus. Since there is no independent evidence for or against this view at the moment, it appears to be most parsimonious to assume that the condition seen in *Mixosaurus* is plesiomorphic.

- The interpterygoid fenestrae must have been large. They are small to slit-like in all adequately known Triassic ichthyosaurs other than *Mikadocephalus*.
- The posteromedial processes of the pterygoids, which are present in mixosaurids and shastasaurids, are lacking in *Mikadocephalus* as in all post-Triassic ichthyosaurs in which the pterygoid is known.
- The pterygoids surely did not meet below the basis cranii, as they do in *Mixosaurus* (von Huene 1916; pers. obs.).

Some of these characters are uniquely shared with the post-Triassic ichthyosaurs; these are:

– the large interpterygoid fenestrae;

– the lack of the posteromedial process of the pterygoid.

The probable relationships of the best known Triassic and Jurassic forms can be set up as follows (Fig.8, Tab.1):

Characters

1 Maxilla reaches external narial opening yes 0 no 1
2 Maxilla with postnarial process yes 0 no 1
3 Lacrimal reaches external narial opening yes 0 no 1
4 Premaxilla with processus supranarialis no 0, yes, forms much less than ½ of upper external narial margin, 1, yes, forms more than ½ of the upper narial margin 2
5 Nasal ends in front of or at the level of the anterior margin of the orbit 0, reaches back above the orbit up to about mid-orbital level 1
6 Frontal does not reach temporal opening 0, reaches temporal opening 1
7 Temporal opening tiny, slit-like 0, large, at least 1/3 the size of the orbit 1
8 Squamosal separately ossified 0, fused to quadratojugal or lost 1
9 Nasal reaches postfrontal no 0, yes 1
10 Nasal reaches supratemporal no 0, yes 1
11 Dentition in maxilla thecodont 0, aulacodont/thecodont 1, exclusively aulacodont 2
12 Dentition in premaxilla and dentary aulacodont 0, thecodont 1. The primitive character state is present in *Utatsusaurus* (Motani 1996) and *Mixosaurus* pers. obs., which makes this coding the most parsimonious
13 Dentition slightly heterodont 0, isodont 1
14 Foramen arteria carotici interna posterius unpaired 0, paired 1
15 Parasphenoid with bony collar reaching back to vover basioccipital ventrally 0, without this 1
16 Frontal as large or larger than parietal 0, distinctively smaller 1
17 Premaxilla reaches jugal no 0, yes 1
18 Pterygoid overlaps palatine ventrally no 0, yes 1
19 Processus quadratus small, not clearly set off 0, long, quadrate facet sitting on bony collar, directed posteriorly 1, hook-shaped, directed medially 2
20 Pterygoid with posteromedial process yes 0, no 1
21 Pterygoids meeting below basis cranii yes 0 no 1
22 Interpterygoid fenestra small 0, large 1
23 Occipital condyle convex 0, concave 1
24 Jugal-quadratojugal notch distinctive 0, secondarily closed 1
25 Extensive occipital flange of supratemporal no 0 yes 1
26 Postorbital skull segment as long or longer than orbit 0 much shorter than orbit 1
27 Maxilla from posterior narial border forwards more than 20 % 0 less than 20 % skull length 1

Tab. 1. Character matrix for cladogram presented in Fig. 8.

	Mc	*Cp*	*Mg*	*Tt*	*Ic*	*Sq*	*Oi*	*Bn*
1	0	0	0	1	1	1	0	0
2	0	0	0	1	1	1	1	1
3	0	0	0	1	1	1	1	1
4	0	2	1	1	1	1	1	1
5	0	1	1	1	1	1	1	1
6	0	1	0	0	0	0	0	0
7	0	1	1	1	1	1	1	1
8	0	0	0	0	1	0	0	0
9	0	1	?	1	1	1	1	1
10	0	1	0	0	0	0	0	0
11	0	0	1	2	2	2	2	2
12	0	1	?	0	0	0	0	0
13	0	1	0	1	1	1	1	1
14	0	?	1	1	0	1	0	0
15	0	?	0	1	1	1	1	1
16	0	1	1	1	1	1	1	1
17	0	0	0	1	0	0	0	0
18	0	1	0	0	0	1	1	1
19	0	1	1	2	1	0	0	0
20	0	0	1	1	1	1	1	1
21	0	1	1	1	1	1	1	1
22	0	0	1	1	1	1	1	1
23	0	1	0	0	0	0	0	0
24	0	0	0	1	0	0	0	0
25	?	0	1	1	1	1	1	1
26	1	0	0	0	1	1	1	1
27	1	0	0	0	1	1	1	1

Taxa

1. *Mixosaurus cornalianus* (Bassani 1886) (pers. obs.)
2. *Cymbospondylus petrinus* (Leidy 1868) (data from Merriam 1908)
3. *Mikadocephalus gracilirostris* Maisch & Matzke; pers. obs.
4. *Temnodontosaurus trigonodon* (von Theodori 1843) pers. obs.
5. *Ichthyosaurus communis* (Conybeare 1822); (Sollas 1916; Mc Gowan 1973; pers. obs.)
6. *Stenopterygius quadriscissus* (Quenstedt 1856) pers. obs.
7. *Ophthalmosaurus icenicus* (Seeley 1874) (Andrews 1910; pers. obs.)
8. *Baptanodon natans* (Marsh 1879) (data from Gilmore 1905)

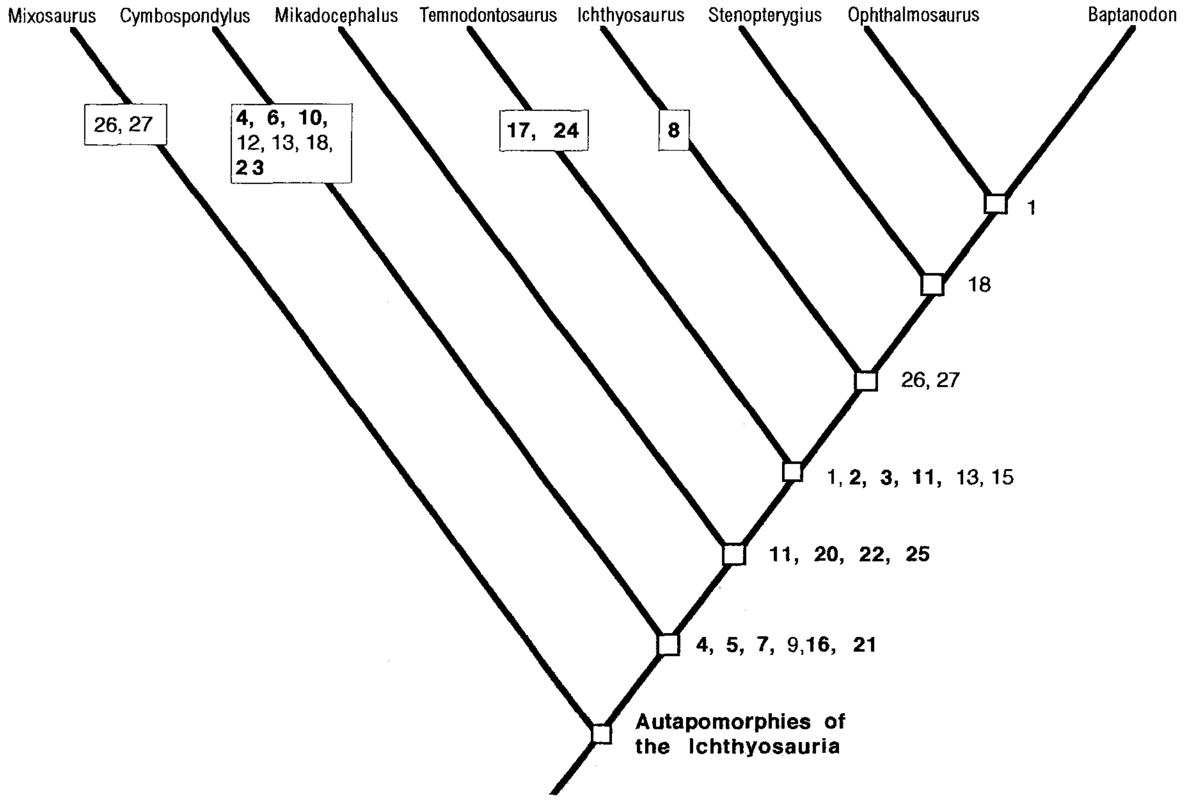

Fig. 8. Phylogenetic argumentation scheme of the Ichthyosauria.

Acknowledgements

Our sincere thanks go to Prof. Dr. Wolf-Ernst Reif and Prof. Dr. Frank Westphal, Tübingen, for their constant support and encouragement, as well as to Dr. David Gower who critically reviewed the manuscript. Wolfgang Gerber kindly took the excellent photographs. Stimulating discussion with the entire Tübingen Vertebrate Research Group helped much to improve the quality of the manuscript. Our sincerest thanks go to Fritz Lörcher for the time-consuming and absolutely excellent preparation of the valuable specimen. This study has benefited more from his expertise in fossil preparation than from anyone else's contributions.

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Eingang des Manuskriptes am 18. Februar 1997;
Annahme durch die Schriftleitung am 10. Juli 1997