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Revision of *Ceratodus concinnus* PLIENINGER

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With 1 plate and 3 textfigures

Summary

Ceratodus concinnus PLIENINGER 1844 from the German Middle Keuper is a valid species represented by tooth plates. Unworn plates are cutting and worn plates are crushing ones. *C. silesiacus* ROEMER 1870, *C. gypsatus* QUENSTEDT 1885, and *C. margatus* QUENSTEDT 1885 are junior synonyms of *C. concinnus*. This species belongs to the same evolutive lineage as *C. rectangulus, C. phillipsi, Asiaceratodus sharovi, C. donensis,* and *C. serratus*. The juvenile tooth plates of these different species are very similar.

Zusammenfassung

Ceratodus concinnus PLIENINGER 1844 aus dem deutschen Mittelkeuper ist eine auf Zahnplatten basierende, valide Art. Nicht abgenützte Zahnplatten waren schneidend, abgenützte quetschend. *C. silesiacus* ROEMER 1870, *C. gypsatus* QUENSTEDT 1885 und *C. margatus* QUENSTEDT 1885 sind jüngere Synonyme von *C. concinnus*. Diese Art gehört zum gleichen Evolutionszweig wie *C. rectangulus, C. phillipsi, Asiaceratodus sharovi, C. donensis* und *C. serratus*. Die juvenilen Zahnplatten dieser verschiedenen Arten sind einander sehr ähnlich.

Contents

1. Introduction

The species *Ceratodus concinnus* was erected by PLIENINGER (in MEYER & PLIENINGER 1844) for two lower tooth plates. One (pl. 11, fig. 9a and 9b) was well preserved and the second one (pl. 11 fig. 9c) had lost its first and fifth ridges. These remains were fixed to the splenial bone (JARVIK's terminology 1967). On the former the symphysial part was lacking and on the latter this bone, except for the articular posterior part, was complete but its mesial bony layer was scrapped. PLIENINGER has not clearly chosen the holotype. After PLIENINGER no paleontologist has given a new description of these remains which were but rarely cited in the literature. PEYER (in STROMER & PEYER 1917) cited this species and stated that it had to be studied again. The two specimens are kept in the collections of the Staatliches Museum für Naturkunde in Stuttgart together with about 30 others which were discovered at different localities.

1.1. Geological occurence

PLIENINGER (1844) wrote that the Middle Keuper of the Stuttgart region has yielded the *C. concinnus* tooth plates of his collection but he has not given exact data about the locality and the stratigraphy. I am greatly indebted to Dr. O. LINCK who has friendly communicated to me some informations about this material. Dr. LINCK himself has collected *C. concinnus* tooth plates in a locality near Sonnenbergstrasse in Stuttgart (Bopser, Southern part of the town) in the lower part of the Bunte Mergel (Lehrbergbänke). The tooth plates of the PLIENINGER collection come from the same locality (the original labels indicate also the locality Stuttgart, Bopser). This locality and the stratigraphic horizon are different fom the outcrops of the Upper Keuper (Rhetian) of Sonnenberg (Soutwestern part of Stuttgart).

C. concinnus is present in the Upper Muschelkalk (Grenzbonebed of Crailsheim), in the upper Lettenkeuper (Hohenecker Kalk), and has been discovered probably also in the Gipskeuper (ENGEL 1906). The geologically youngest tooth plates of *C. concinnus* were found in the Blasensandstein of Franconia (= Kieselsandstein in Württemberg) which is slightly younger than the Lehrbergbänke of Baden-Württemberg. More than 60 tooth plates were found in the Blasensandstein before the second world war (O. KUHN 1936) but this material is lost.

2. Description

Terminology

Fig. 2

Most lungfish tooth plates are more or less triangular and bear ridges. Often these ridges radiate from one angle of the plate. One edge of this angle is formed by one ridge. This is the mesial edge, and this ridge will be called the first one. This angle is the inner angle (innerer Winkel of German paleontologists). The second edge of the inner angle is the lingual edge. The ridges which are running along this edge are called last ridges. The third edge of the triangle bears the tips of the ridges. It will be called the labial edge.

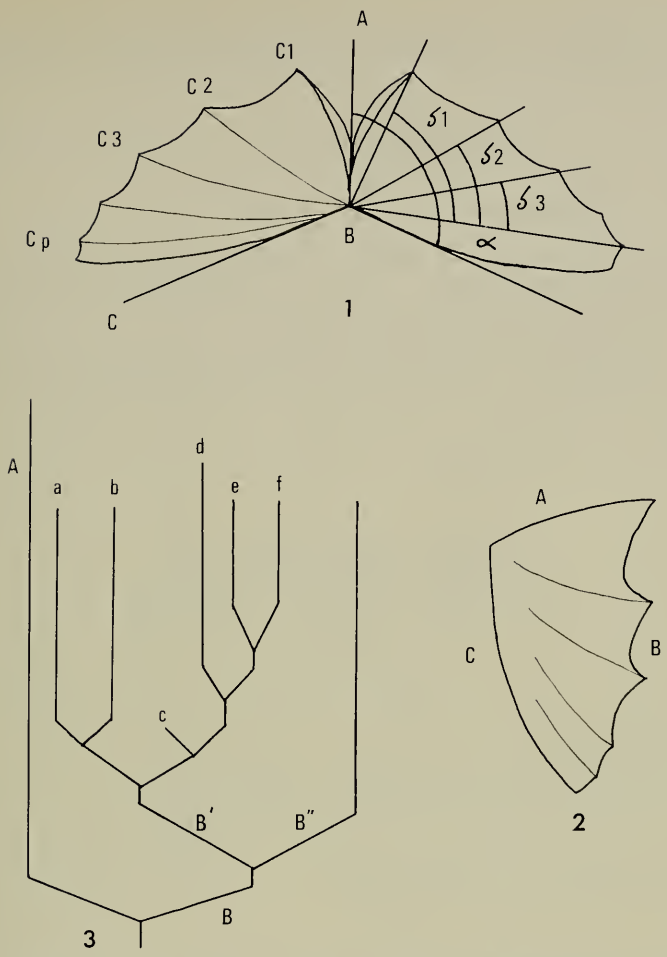

Fig. 1. Measurements: inner angle. — 1: inner angle of the first ridge; 2: inner angle of the second ridge; 3: inner angle of the third ridge.

Fig. 2. Terminology. — A: mesial edge; B: labial edge; C: lingual edge.

Fig. 3. Phyletic tree. — A: *Arganodus* group; B": *Ceratodus kaupi* group; B': *Ceratodus serratus* group; a: *C. serratus*, b: *C. donensis*, c: *Asiaceratodus sharovi*, d: *C. phillipsi*, e: *C. rectangulus*, f: *C. concinnus*.

Method of study
(Vorobjeva & Minikh 1968)

About 100 tooth plates were studied statistically and biometricalli by Vorobjeva & Minikh (1968). They measured the angles and lenghts, mainly of the ridges, to obtain indices. By their method it was possible to separate 3 species. Their method is applied here.

The following angles were measured (fig. 1):

1. The inner angle of the plate (ABC = α) formed by the mesial and lingual edge of the plate.

2. The internal angle of the first, second, and third ridge (δ 1, δ 2, δ 3), which is measured, respectively, between these ridges and the most lingual (i. e. last) one.

The following indices are used (fig. 1):

1. The index of length of ridges BC1/BCp, BC2/BCp.
2. The index of length of the first ridge BC1/BC2.
3. The indices of width of the notches C1C2/C1Cp, C2C3/C2Cp.
4. The index of length of the labial edge (outer margin of Vorobjeva & Minikh) C1Cp/BCp and the auxiliary one C2Cp/BCp.

In the original paper in Russian the unit of angle measurement is grade. In the American translation, howewer, the unit is degree but the conversion from grades to degrees is not made.

Subclass Dipnoi Müller 1844
Family Ceratodontidae Gill 1872
Genus *Ceratodus* Agassiz 1838

Ceratodus concinnus Plieninger 1844

*1844 *Ceratodus concinnus* Plieninger, p. 85/86, pl. 10, fig. 9a, b, c.
1870 *Ceratodus silesiacus* Roemer, p. 184, pl. 15, fig. 6, 7.
1885 *Ceratodus margatus* Quenstedt, pl. 24, fig. 1.
1885 *Ceratodus gypsatus* Quenstedt, pl. 24, fig. 2.

Lectotype: Plieninger 1844, pl. 11, fig. 9a, b; SMNS 51107, designated herein.

Stratum typicum: Middle Keuper.

Locus typicus: Stuttgart, Bopser.

Material: 32 tooth plates in the Staatliches Museum für Naturkunde in Stuttgart (Ludwigsburg; abbreviation SMNS) and the holotypes of *C. margatus* and *C. gypsatus* in the Institut und Museum für Geologie und Paläontologie of the University of Tübingen. Numbers (SMNS, Ludwigsburg): 11032, 11422, 12418, 12707, 12708, and 51107, 51123 (all from Stuttgart, Bopser); 51146 from Crailsheim and 51145 from Hoheneck.

Description of the lectotype (pl. 1, fig. a): It is a lower right tooth plate which is borne by the well preserved posterior part of the splenial bone. The apex of the inner angle is well marked. The inner angle itself amounts to about 100°; the tooth plate bears 4 ridges which radiate from the apex of the inner angle. The first ridge and the second are straight but the two last are slightly curved laterally. The mesial edge is straight and the lingual one follows the curvature of the last ridge after the third quarter of its length. The mesial edge is almost so long as the lingual. The first notch between the first and the second ridge is not broader than the second between the second and the third ridge. In their unworn parts the ridges are sharp. The region of the apex of the inner angle is worn and the first ridge rises sharply above this eroded part; the other ridges become gradually higher from the second to the fourth. The un-

worn part of the ridges bears small acute denticles. The enamel tissue is preserved on these parts of the ridges and in the notches. The number of „teeth" of *C. concinnus* allows to understand the growth of the tooth plates and to record the individual variation of morphology as well as those morphological variations which are caused by the wear of the tooth plates.

Differences between lower and upper tooth plates

1. The tooth plates display a distinctive character (restricted to the species *C. concinnus*): the upper tooth plates (pl. 1, fig. g) have a mesial edge shorter than the lingual edge, the lower tooth plates have a mesial edge almost as long as the lingual one (pl. 1, fig. i) except for some plates in which the mesial edge is shorter but never as short as that of the palatal tooth plates (pl. 1, fig. k). This long first ridge is a primitive character.

2. The mesial side of the first ridge of the upper tooth plates is worn by a more or less developped area caused by the contact between the two symmetrical tooth plates. This character is absent in lower tooth plates of *C. concinnus*.

3. We can distinguish the upper and lower tooth plates in all species of European ceratodontids, in *Neoceratodus forsteri* Krefft 1870, in African Cretaceous Dipnoans, in *C. madagascariensis* Priem 1924, and in *Arganodus atlantis* Martin 1979b in the same way: the first ridge of a splenial tooth plate has a convex mesial side which is visible from above (pl. 1, fig. g); the mesial side of the first ridge of upper tooth plates remains invisible in the same position (pl. 1, fig. a, i, j, k).

The angle between the plane of the occlusal surface of the tooth plate and the mesial side of the first ridge is acute for an upper and obtuse for a lower tooth plate. The side view of the lingual and the labial edge of the lower tooth plates is straight or slightly concave, and posteriorly deep, this side view is convex and low in the upper tooth plates. This difference of the "profil mesialolingual" was previously recorded by Tabaste (1963).

The occlusion

pl. 1, fig. o

The first ridges of the lower symmetrical tooth plates are not in contact, the first two ridges of the upper tooth plates come between them, meanwhile the first lower ridges come into the first upper notch and so on (this disposition is known in all ceratodontids).

General morphological pattern of the tooth plates

Most tooth plates are rather similar to the lectotype: they are rather large (BCI = 26 mm, BCp = 30 mm) with four or five radiating ridges. The inner angle is usually equal to 105°. The unworn part of the ridges is sharp and bears small denticles (pl. 1, fig. f). These denticles are present on the vertical labial tips of the ridges (pl. 1, fig. b′). On some tooth plates instead of the fifth ridge the convex lingual edge is more developped. This part of the tooth plate bears a kind of rounded low and broad enlargement which seems a poorly developped „embryo" of fifth ridge. This structure is always rounded even when the four other true ridges are sharp (pl. 1, fig. i).

The different degrees of wear

1. Description of a small juvenile, unworn plate (nr. 51111; pl. 1, fig. c). This tooth plate is a small (BCI = 5,5 mm; BCp = 7,5 mm) upper left one. The inner angle is equal to about 105° and the length of the first ridge is equal to $^2/_3$ of the length of the lingual edge which is straight. The ridges are straight, except the fourth one which is slightly curved laterally. The first three ridges are radiating from the apex of the inner angle which is well marked. The ridges bear small broken denticles.

2. Some tooth plates are little worn and look like the young, small tooth plate. The ridges are sharp and bear denticles (nr. 5115a; pl. 1, fig. f).

3. First the wear abrades the region of the apex of the inner angle. The ridges become rounded in their worn part. Their unworn part stays cutting and sharp. The enamel tissue disappears in the worn part of the tooth plate (nr. 51121; pl. 1, fig. g).

4. The rounded part reaches the labial end of the ridges. The denticles are only remaining on the labial vertical part of the ridges. There is no remaining enamel tissue except in the labial low part of the notches (nr. 11422; pl. 1, fig. k).

5. The first rounded ridge is always present in the lower tooth plates; meanwhile the contact between the symmetrical tooth plates and the wear gives a cutting aspect to the first ridge of the upper tooth plates (pl. 1, fig. b, k). There is no remain of the course of ridges except a low tubercle on the labial edge of the tooth plate. The labial part of these tubercles may be rather cutting. These very worn plates seem very crushing.

Range of variability of the tooth plates

The variation in size is given by table 1 (lenght of BCp). The inner angle varies from 90° to 125° what is not uncommon for the ceratodontids. The most important aspect of this variation deals whith the appearence of some plates which have an "embryo" of fifth ridge: when they begin to be worn, these plates look very much like a small typical plate of *C. kaupi* Agassiz 1838 (nr. 11422); but they do not belong to this species since there are several remains (nr. 51109 and nr. 51110) which show how the wear gives gradually this appearence to the tooth plate (pl. 1, fig. i, j, k).

The splenial and the palatopterygoid

The splenial (nr. 11032; pl. 1, fig. p) is a thick (3 mm) bone which has the typical shape of the ceratodontid splenial (Jarvik 1967, Martin 1979a). Its inner side bears a vertical ridge below the first notch, between the first and the second ridge of the tooth plate (pl. 1, fig. p). This kind of ridge is present in the same position on the splenial of *C. phillipsi* Agassiz 1838 (Martin et al., in press) and *C. madagascariensis* Priem 1924 (Martin 1979a). This structure is the remain of the Ruge's canal (Jarvik 1967, Martin 1979a). The thickest and strongest part oft the splenial is the symphysial part of the bone which joins with the symmetrical bones approximately on the longitudinal axis of the lower jaw.

What remains of the palatopterygoid is a flat and long plate fixed to the tooth plate on its lingual edge (nr. 12708; pl. 1, fig. b). The pterygopalatine process arises from the dorsal surface of the tooth plate to join with the skull roof. This process is above the second ridge (nr. 51112; pl. 1, fig. o); this position is very common (MARTIN 1979a).

The ceratohyal
pl. 1, fig. q

It is a long cylindrical bone; the distal end is lacking. The proximal end is flattened and larger. This bone is similar to that of *Neoceratodus forsteri* KREFFT 1870 (GUNTHER 1871) and of *Arganodus atlantis* MARTIN 1979 (pl. 1; fig. q, r, s).

3. Comparisons

3.1. Comparison with European Triassic ceratodontids

Ceratodus kaupi AGASSIZ 1838

This species is present during the whole Triassic. When worn some tooth plates of *C. concinnus* are similar to those of this species (pl. 1, fig. k). The shape is similar mainly because of the worn rounded crushing ridges, because of the worn rounded "embryo" of fifth ridge and, on the lower tooth plates, because of the length of the first ridge. There are slight differences between the *C. concinnus* tooth plates and the *C. kaupi* tooth plates:

1. The labial vertical part of the ridges bears denticles on the *C. concinnus* tooth plates.
2. The tooth plates of *C. concinnus* are usually smaller than the tooth plates of *C. kaupi,* except for small, juvenile tooth plates but they are usually less worn.
3. The radiating pattern of the ridges is almost always visible on the tooth plates of *C. concinnus;* this radiating pattern disappears easily on the *C. kaupi* tooth plates.

Are these similarities evidences for phyletic relationships between *C. concinnus* and *C. kaupi*?

The tooth plates of *C. humei* PRIEM 1914 (Lower Cretaceous of Africa) when they are worn are very similar to those of *C. kaupi* (pl. 3, fig. 3, 4, 5, 6, 7 in ARAMBOURG & JOLEAUD 1943) and there is no evidence of phyletic relationships between *C. kaupi* and *C. humei.*

A poorly developped seventh ridge may be present on the tooth plates of *C. africanus* HAUG 1904. This "embryo" of ridge looks very much like this "embryo" of fifth ridge of *C. concinnus* tooth plates. I believe that these similarities between *C. concinnus* and *C. kaupi* are the result of a convergence.

Ceratodus rectangulus LINCK 1936

This species is yielded by the Stubensandstein (Middle Keuper). The tooth plates of it bear the same kind of rounded ridges when they are worn. The labial tubercle is present as on the corresponding tooth plates of *C. concinnus,*

this tubercle is usually a cutting one. The proportions of the tooth plates are slightly different: mainly the lower tooth plates of *C. rectangulus* are longer than those of *C. concinnus* (pl. 1, fig. h).

According to LINCK's measurements (LINCK 1936) the inner angle of *C. concinnus* tooth plates is larger than the inner angle of *C. rectangulus* tooth plates. But on the other hand the first ridge of the lower tooth plates of *C. rectangulus* looks very much like that of the *C. concinnus* tooth plates. These two species likely belong to the same evolutive lineage of ceratodontids.

Ceratodus serratus AGASSIZ 1838

This ceratodontid is very common in the German Triassic. The large tooth plates of *C. serratus* do not exhibit the same pattern as the large ones of *C. concinnus* which have never 6 true ridges. The *C. serratus* tooth plates are always longer and look always more cutting than the tooth plates of *C. concinnus*. The worn part of the ridges of the *C. serratus* tooth plates is never as rounded as this part of the *C. concinnus* ones (pl. 1, fig. n).

Ceratodus priscus E. FRAAS 1904

Two small "teeth" from the Middle Buntsandstein of the Wildbad region are referred to this species. The holotype (SMNS nr. 11146) and the second specimen (SMNS nr. 15441) are only the impression of the tooth plates in the sandstone. They were small tooth plates (BCp = 14,5 mm). They exhibit a radiating pattern of cutting ridges. The first ridge is about equal $^2/_3$ of the lingual edge, and the inner angle is about equal to 90°. These tooth plates fit rather well with the smallest tooth plates referred to *C. concinnus*.

Ceratodus palaeoruncinatus FRENTZEN 1924

This species is represented by only one tooth plate from the Upper Buntsandstein of the Karlsruhe region. According to FRENTZEN's figure and measurements this tooth plate fits very well with the *C. priscus* tooth plates. Only the inner angle of the former tooth plate is slightly larger, about 110° (it is not as large as FRENTZEN himself has written: 135°). This tooth plate is likely a larger tooth plate of the same species as that to which the *C. priscus* ones belong. But the *C. palaeoruncinatus* tooth plate fits, too, very well with the tooth plates of *C. serratus*. These tooth plates from the Lower Triassic are likely junior synonyms of *C. serratus*.

Ceratodus phillipsi AGASSIZ 1838

This species was described as *C. parvus* by QUENSTEDT 1885 and PEYER 1917 (MARTIN et al. 1981). This species is present in Western Europe from the Upper Triassic to the Middle Jurassic. The smallest plates of it are very similar to the small tooth plate of *C. concinnus* (nr. 51111). The larger ones are different. Those of *C. phillipsi* are always longer and more cutting than the *C. concinnus* tooth plates (MARTIN et al. 1981). There is never, on the *C. phillipsi* tooth plates, a poorly developped "embryo" of fifth ridge (pl. 1, fig. d).

Ceratodus silesiacus ROEMER 1870

ROEMER referred to this species of the Upper Triassic of Breslau region a small tooth plate (pl. 15, fig. 6) and a large tooth plate (pl. 15, fig. 7). The smallest tooth plate fits very well with the smallest tooth plate of *C. concinnus:* the radiating pattern of the cutting ridge is the same. The morphology of the latter is very similar to the morphology of the *C. concinnus* tooth plates which bear a fifth poorly developped ridge. *C. silesiacus* is surely a junior synonym of *C. concinnus*. This referal to *C. concinnus* is strengthened by ROEMER's correlations. This author correlated the level in which the tooth plates of *C. silesiacus* were discovered with the Bunte Mergel which yielded most *C. concinnus*.

Ceratodus margatus QUENSTEDT 1885

This lower tooth plate — from the Middle Keuper of Murrhardt (pl. 24, fig. 1a, b) — is a typical one of *C. concinnus:* the length of the first ridge is almost the same as the length of the lingual edge, the radiating pattern of the rounded worn ridge is present, and the cutting labial part of these ridges bear small denticles. The splenial itself exhibits the same ridge, under the first notch, as in the typical splenial of *C. concinnus*.

Ceratodus gypsatus QUENSTEDT 1885

This specimen from the Lettenkeuper of Crailsheim region (pl. 24, fig. 2) is a typical large tooth plate of *C. concinnus*: the proportions (BCI = $^2/_3$ BCp) are the same, the radiating pattern of the 5 ridges is the same and there are, too, small denticles on the labial cutting vertical part of the ridges. *C. margatus* and *C. gypsatus* are junior synonyms of *C. concinnus*.

3.2. Comparison with the ceratodontids from the Triassic of Siberia

Asiaceratodus sharovi VOROBJEVA 1967

This small ceratodontid from the lower Triassic is represented by complete skeletons with well preserved skull roofs and tooth plates. The tooth plates (textfig. 5) with 4 or 5 cutting denticulated ridges are rather similar to some unworn plates of *C. concinnus*. The main difference is the lower inner angle which does not exceed 72°.

Ceratodus donensis VOROBJEVA & MINIKH 1968

The first ridge of the lower tooth plates, known from the Lower to the Upper Triassic (pl. 1, fig. 10 to 22) is about as long as the lingual edge, but these plates have always cutting ridges and the upper plates bear sometimes a sixth ridge. These Siberian tooth plates are not very different from the typical *C. concinnus* tooth plates.

All the tooth plates of these different valid species of ceratodontids are only slightly different from the *C. concinnus* tooth plates. Do they belong to the same evolutive group?

The tooth plates of the Devonian lungfishes bear always a first ridge which is the longest, and the radiating pattern of the ridges or of the rows of tubercles

is always visible. Most Devonian tooth plates bear between 8 and 10 true ridges or rows of tubercles. The *C. kaupi* tooth plates bear never more than 5 ridges. Even on the small, likely juvenile tooth plates the radiating pattern of the ridges is almost lost. The ridges are always crushing ones and the first ridge is often the longest. These characters are visible on the small tooth plates which can be easily referred to this species.

On the other hand the tooth plates of *C. concinnus*, *C. rectangulus*, *C. phillipsi*, *Asiaceratodus sharovi*, *C. serratus*, and *C. donensis* bear between 4 and 6 ridges, at least on the upper tooth plates; the first ridge is the shortest (or as long as the second one), the ridges are cutting during most part of the life of the lungfish and a primitive character is well visible, the radiating pattern of the ridges.

This pattern is quite different from that which is exhibited by the *C. kaupi* plates, and the mentioned ceratodontids likely belong to the same evolutive group, the most important trends of which are the following ones:

1. loss of at least the seventh ridge,
2. shortening of (at least) the first upper ridge,
3. presence of cutting ridges.

The small juvenile upper tooth plates strengthen this gathering. The morphology alone cannot permit the referal of these small tooth plates to different species. The small *C. concinnus* tooth plate nr. 51111 is quite similar to the small juvenile tooth plates of *C. rectangulus*, *C. phillipsi*, and *C. serratus*. They exhibit the same radiating pattern of cutting ridges, the same first ridge, and the same proportions (MARTIN et al., in press).

I think that there are at least three different evolutive groups of ceratodontids during the Triassic. In the first one, the group of *Arganodus*, the number of the ridges is always primitive (at least 7), in the *C. kaupi* group there are never more than 5 crushing ridges and the radiating pattern is lost, in the *C. serratus* group there are less than 7 cutting ridges and the first upper ridge is short.

3.3. Biometry

Table 1.

BCp	α	$\delta 1$	$\delta 2$	$\delta 3$	$\frac{BC2}{BC1}$	$\frac{BC1}{BCp}$	$\frac{C1Cp}{BCp}$	$\frac{C1C2}{BC1}$	$\frac{C1C2}{C1Cp}$	$\frac{C1C2}{BCp}$	$\frac{C2C3}{C2Cp}$		
40 mm	130°	85°	60°	35°	112	99	150	66	50	58	72	max.	*C. concinnus*
	105°	77°	46°	27°	97	78	110	50	42	42	52	m.	
7,5	83°	65°	40°	20°	78	60	90	36	26	26	36	min.	
7,5	105°	75°	55°	35°	92	73	112	42	30	33	41	1 ex.	nr. 51111
24	115°	85°	60°	35°	97	71	117	48	35	33	40	1 ex.	*C. gypsatus*
24	105°	75°	50°	20°	114	80	104	55	44	48	50	1 ex.	*C. margatus*
	101°	93°	61°	30°	99	62	118	62	33	36	50	m.	*C. phillipsi*
													C. priscus
	83°	80°	55°	30°	100	68	103	45	30	31	38	1 ex.	nr. 11146
	95°	85°	59°	34°	100	80	120	50	33	40	47	1 ex.	nr. 15441
	113°	—	—	37°	107	90	102	68	—	—	61	max.	*C. donensis*
	78°	—	—	20°	82	65	80	53	—	—	55	min.	

The measurements and indices of *C. donensis* are those of VOROBJEVA & MINIKH 1968.

The biometry gives some evidences for distinguishing *C. concinnus* and *C. kaupi*: in the former the inner angle and the inner angle of the second ridge are slightly smaller than in the latter (105° and 46° against 112° and 54°); the index C2C3/C2Cp is larger in *C. concinnus* than in *C. kaupi* (52 % against 45 %). These results were obtained from the measurements of about 80 complete tooth plates of *C. kaupi* from the locality Hoheneck displaying all sizes. The most important result is the difference between the index BC1/BCp which is smaller — only 78 % — in *C. concinnus* and more than 95 % in *C. kaupi.*

There are some evidences, too, for separating *C. concinnus* from *C. phillipsi*, *C. serratus*, and *C. donensis*. The main difference between *C. concinnus* and *C. phillipsi* is the inner angle of the first ridge; in *C. concinnus* it reaches 85 °: this is the smallest in *C. phillipsi.* On the small plate nr. 51111 which is quite similar to the typical plates of *C. phillipsi* the inner angle is only 75 °; this measurement permits the referal of this tooth plate to *C. concinnus.*

The main differences between *C. concinnus* and *C. serratus* are the inner angle of the second ridge and the index C1C2/C1Cp (46° and 42 % against 56° and 31 %).

The main difference between *C. concinnus* and *C. donensis* is the index C1Cp/BCp; only three plates of *C. concinnus* give an index smaller than the largest index (102 %) of *C. donensis.*

One index is rather interesting for the phylogeny: the mean value of the index BC1/BCp is equal to 64 in *C. rectangulus*, 66 in *C. serratus* and *C. phillipsi*, 78 in *C. concinnus* and 97 in *C. kaupi.* This index indicates that the first ridge of the tooth plates of *C. kaupi* is at least as long as the lingual edge in about 50 % of the tooth plates. This first ridge is shorter in about 85 % of the *C. concinnus* tooth plates and it is always shorter in the other species.

These indices and measurements cannot take the place of the morphological study but they show the extend of the range of variability and they permit the assignment of untypical tooth plates to different species.

I shall give a diagnosis of *Ceratodus concinnus* though this purpose is difficult because of the range of variability of this species.

4. Diagnosis

Ceratodontid with tooth plates exhibiting a radiating pattern of 4 or 5 cutting ridges; the first lower ridge may be as long as the lingual edge, the inner angle varies between 85° and 130°; a poorly developped rounded ridge may be present; the ridges bear denticles, and when they are worn they look like crushing ones. The splenial bears a vertical ridge below the first notch.

5. Paleoecology and paleoethology

Only one minute tooth plate was collected with the larger ones from the Stuttgart, Bopser locality: this fact could show that the young specimens of this species did not live in the same biotope as the large, older ones. We cannot assume this opinion with certainty because the smallest tooth plates perhaps were not collected on account of their size.

The Lehrbergbänke were deposited in marine environment. The tooth plates of *C. concinnus* which were preserved in this layer are not rolled. Obviously this population of *C. concinnus* was living in littoral marine water. If the absence of small, young specimens is truly the result of life in different biotopes it would be possible to assume that the eggs were laid in freshwater, and that the young specimes lived in quiet freshwater before they moved to the littoral water.

6. Results

Ceratodus concinnus is a valid species present in the German Triassic from the upper Muschelkalk to the lower part of the Middle Keuper. This species is mainly represented by tooth plates from the Lehrbergschichten. These tooth plates exhibit a radiating pattern of cutting ridges when the plate is not too worn. This species belongs to the same evolutive group as *C. rectangulus, C. phillipsi, Asiaceratodus sharovi, C. donensis,* and *C. serratus.* The evolutive trends of this group are the loss of (at least) the seventh ridge, the shortening of the first ridge of the upper plates and the presence of cutting ridges. The similarity between the small young tooth plates of those different species gives a good evidence of the existence of this group of ceratodontids. It is possible that the adult *Ceratodus concinnus* lived in marine environment and the young in freshwater.

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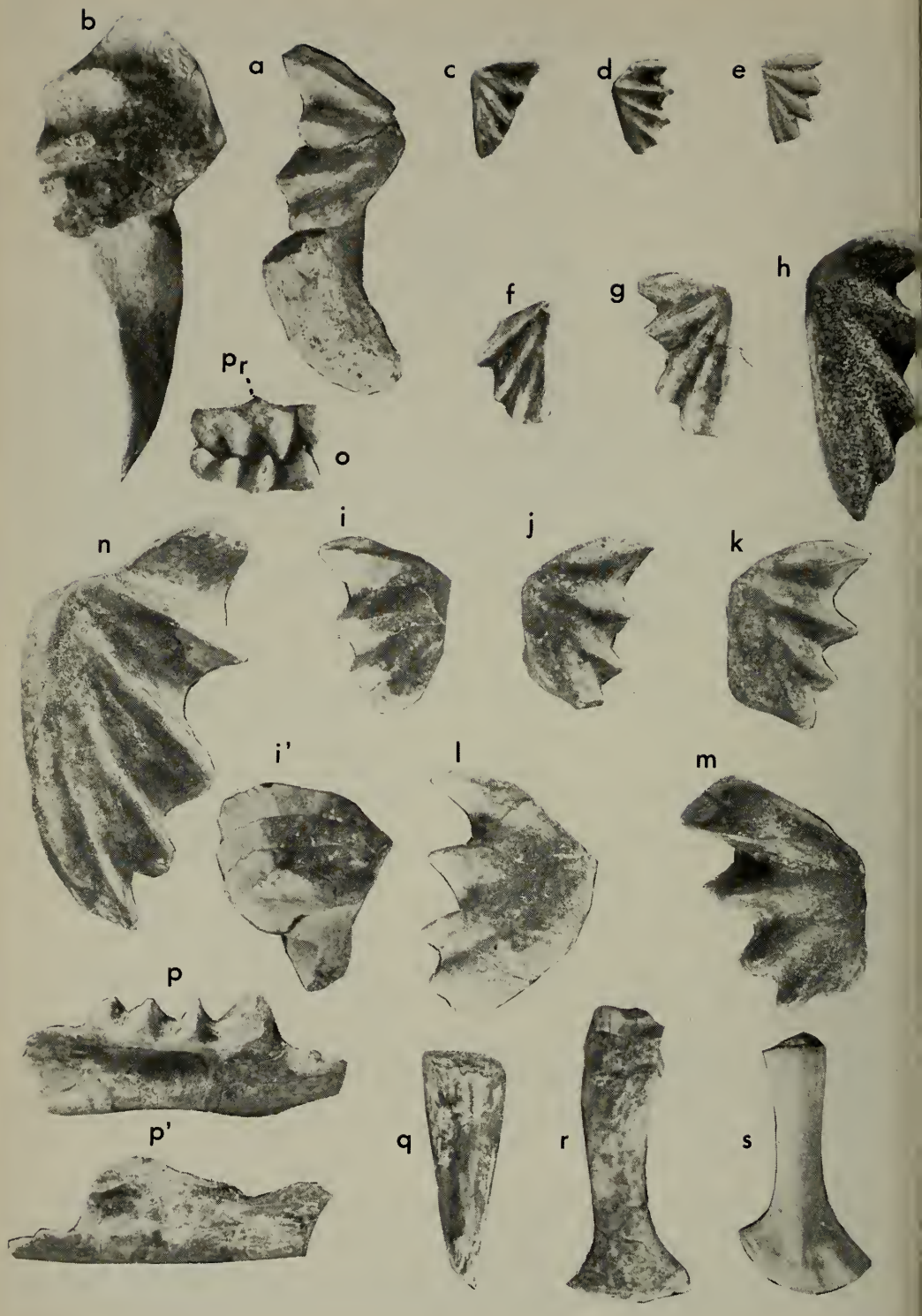

Plate 1

Ceratodus concinnus PLIENINGER (a, b, c, f, g, i, j, k, l, o, p, q).

a: lectotype (l lt); b: worn plate (r ut); c: small juvenile plate (l ut); f and g: larger unworn plates (r ut); i: normal plate (l lt); j: plate with a small lingual enlargement (l lt); k: *C. kaupi* like plate with an "embryo" of fifth ridge (l lt); l: very worn plate (r ut); o: right tooth plates in occlusion (labial view); p: lateral side of the splenial; p': mesial side of the splenial; q: ceratohyal of *C. concinnus;* i': tubercles on the vertical part of the ridges of a worn plate (r ut).
d: *Ceratodus phillipsi* AGASSIZ (SMNS nr. 50930) (l ut);
e: *Ceratodus "priscus"* FRAAS (SMNS nr. 15441) (?);
h: *Ceratodus rectangulus* LINCK (SMNS nr. 17965) (l lt);
m: *Ceratodus kaupi* AGASSIZ (SMNS nr. 51124) (l lt);
n: *Ceratodus serratus* AGASSIZ (SMNS nr. 51125) (l ut);
r: Ceratohyal of *Arganodus atlantis* MARTIN (MNHNP Tal 304 h);
s: Ceratohyal of the living *Neoceratodus forsteri* KREFFT.

Abbreviations: l: left; r: right; lt: lower tooth plate; ut: upper tooth plate; SMNS Staatliches Museum für Naturkunde Stuttgart; MNHNP Museum national d'Histoire naturelle Paris.

All specimens are in natural size except of the small plate (fig. c) which is × 2, and the figure i' which is × 1,5.