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A JUVENILE SPECIMEN OF *EUDIMORPHODON RANZII* ZAMBELLI (REPTILIA, PTEROSAURIA) FROM THE UPPER TRIASSIC (NORIAN) OF BERGAMO

RIASSUNTO: Si descrivono i resti scheletrici di un esemplare giovanile di *Eudimorphodon ranzii* Zambelli provenienti dalle Argilliti di Riva di Solto di età Norica di Ponte Giurino, provincia di Bergamo, Italia. La diagnosi di questa specie di pterosauro, definita dall'autore nel 1978, è completata dall'aggiunta di 3 elementi tarsali; in totale 5 elementi tarsali. L'immaturità dell'esemplare è indicata dalla separazione della scapola dal coracoide, dalla presenza di costole sacrali separate e da vertebre sacrali non fuse, ilio pube ed ischio suturati, tibia e fibula separati, sterno non completamente ossificato e probabilmente composto da interclavicola, entrambe le clavicole ed elementi pari dello sterno, assenza di costole sternocostali fossilizzate. Si descrive per la prima volta la membrana dell'ala di uno pterosauro triassico.

SUMMARY: The skeletal remains of a juvenile specimen of *Eudimorphodon ranzii* Zambelli are described from the Upper Triassic (Norian) bituminous shales of the Argilliti di Riva di Solto of Ponte Giurino, province of Bergamo, Italy. The diagnosis of this pterosaur species, established in 1978 by the author, is supplemented by the addition of 3 more tarsal elements; there are together 5 tarsal elements. The immaturity of the specimen is indicated by the separation of scapula and coracoid, the presence of separated sacral ribs and unfused sacral vertebrae, a sutured ilium, pubis and ischium, a separated tibia and fibula, an incompletely ossified sternum, probably composed of interclavicula, both claviculae and paired sternal elements and the absence of fossilized sternocrostal ribs. The structure of the wing membrane is described for the first time for a Triassic pterosaur.

ZUSAMMENFASSUNG: Aus den obertriassischen (norischen) bituminösen Schiefertonen der Argilliti di Riva di Solto von Ponte Giurino, Provinz Bergamo, Italien, wird der Skelettrest eines jugendlichen Exemplars von *Eudimorphodon ranzii* Zambelli beschrieben. Er ergänzt die vom Autor 1978 gegebene Diagnose dieser Flugsaurier-Art durch den Nachweis von insgesamt 5 Tarsal-Elementen. Die Trennung von Scapula und Coracoid, das Vorhandensein separater Sacralrippen an den nicht miteinander verwachsenen Sacralwirbeln, die Suturverbindung von Ilium, Pubis und Ischium, die Trennung von Tibia und Fibula, das wahrscheinlich aus Interclavicula, beiden Claviculae und paarigen Sternal-Elementen hervorgegangene Sternum, sowie

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fossil nicht überlieferte Sternocostalrippen sind Merkmale des Jugendstadiums. Erstmals werden Struktur und Aufbau der Flughaut eines Trias-Flugsauriers beschrieben.

PAROLE CHIAVE: Triassico Superiore; Norico; Pterosauria; Ontogenesi; Membrana dell'ala; Bergamo; Italia.

KEY WORDS: Upper Triassic; Norian; Pterosauria; Ontogeny; Wing membrane; Bergamo; Italy.

SCHLÜSSELWÖRTER: Obertrias; Nor; Flugsaurier; Ontogenie; Flughaut; Bergamo; Italien.

INTRODUCTION: In early summer 1989 Mr. Angelo Mazzoleni from Stezzano near Bergamo, honorary assistant of the Museo Civico di Scienze Naturali Bergamo, found a small pterosaur skeleton by splitting shales of the Argilliti di Riva di Solto, during an excavation by that museum, at the locality Ponte Giurino in Valle Imagna north of Bergamo. In autumn 1989 offered me the director of that museum, dr M. Guerra, and the curator in geology and paleontology, dr A. Paganoni, this specimen for description. I express my thanks to both colleagues for making it possible to continue my pterosaur studies and for their kind hospitality during my stays in autumn 1991 and spring 1993 at the Bergamo Museum. My gratitude is extended to Mr. M. Pandolfi, preparator of the museum, for technical help and to Mr. F. Zaina, photographer in Bergamo, for taking the photographs.

The pterosaur specimen consists of slab and counter slab. However, parts of the skeleton were lost during splitting; slab and counter slab fit only partly together (Figs. 1-4). Unfortunately the split slab lacks the skull and the tail. Furthermore, the finder had done some provisional preparation which destroyed parts of the wing membranes. Further preparation done by myself nevertheless revealed a rather complete postcranial pterosaur skeleton with partly preserved wing membranes. It is the first Triassic pterosaur pertaining remains of soft tissues, the smallest Triassic Pterosaur hitherto known, and the first pterosaur find from the Argilliti di Riva di Solto Formation. As is shown below the specimen represents a juvenile of the well known species *Eudimorphodon ranzii* Zambelli from the Calcare di Zorzino Formation of the province of Bergamo.

THE UPPER TRIASSIC FOSSIL FAUNA OF PONTE GIURINO AND ITS AGE: The fauna of the Argilliti di Riva di Solto consists of invertebrates and vertebrates. From Ponte Giurino polychaetes (Alessandrello & Teruzzi 1986; Garassino & Teruzzi 1993), few archaeogastropods, some lamellibranchiats. e.g. trigoniids (Zambelli 1986), echinoderm remains, a dragon-fly and remains of coleopterans (Whalley 1986) are known. In contrast, the crustacean fauna is abundant (Garassino & Teruzzi 1993); it also contains the rare thylacocephalian genus *Atropicaris* (Arduini & Brasca 1984). Whereas the crustacean fauna is benthonic and therefore autochtonous, the gastropods and lamellibranchiates seem to be allochthonous and to be dislocated from the carbonate platform situated adjacent to the lagoonal anoxic basins filled with the pelitic shales of the Argilliti of Riva di Solto. The well preserved dragon-fly *Italophlebia gervasuttii* Whalley and the beetle *Holcopteria schlotheimi* (Giebel) came from the adjacent land near Ponte Giurino (Zambelli 1986).

The vertebrate fauna consists mainly of fishes, especially of *Pholidophorus latiusculus gervasuttii* Zambelli. The fishes *Parapholidophorus nybelini* Zambelli and *Pholidoctenus serianus* Zambelli are rare (Zambelli 1975, 1978, 1980, 1986). They represent the necton of the basin. Autochthonous actinopterygian fishes are *Saurichtys* (Tintori & al. 1985) and the "flying" *Thoracopterus magnificus* (Tintori & Sassi 1987, 1992), while the extremely rare *Birgeria* and *Dapedium noricum* Tintori (Tintori 1985) represents allochthonous faunal elements of neighbouring carbonate platforms. The same holds true for the shark *Pseudodalatias barnstonensis* (Sykes), as documented by isolated teeth and tooth batteries at Ponte Giurino (Tintori 1980). The few reptile specimens were washed into the lagoon from the land and are therefore also allochthonous. The tail of a juvenile reptile specimen supposed to belong to *Drepanosaurus unguicaudatus* Pinna, hitherto known through several specimens from the Calcare di Zorzino (Pinna 1980, 1984), turns out to belong to *Megalancosaurus preonensis* Calzavara, Muscio & Wild (Calzavara & al. 1981; Renesto, in press). This small thecodont reptile had an arboreal mode of life, pointing to a continental or island habitat adjacent to the basin. The new juvenile *Eudimorphodon* specimen, too, confirms the terrestrial vicinity to the basin, since juvenile pterosaurs must have developed and lived on land. The complete preservation of the new pterosaur skeleton additionally excludes a transport from a farther distant land.

While the paleogeographic and paleoenvironmental development of the Lombardian Upper Triassic carbonate platforms and their basins seem to be settled (Tintori, 1991; Garassino & Teruzzi 1993; Jadoul & al. 1992; Stefani & al. 1992), the stratigraphic age of the Calcare di Zorzino is still open to debating. Stefani & al. (1992) date the Argilliti di Riva di Solto to be Norian/Rhaetian. By ammonite finds in the Calcare di Zorzino and the Calcare di Zu I concluded that the Argilliti di Riva di Solto are Upper Norian (Wild, 1989; see also Jadoul & al., 1992). MCSNB 8950, clearly a juvenile specimen of *Eudimorphodon ranzii*, rather confirms a Norian than a Rhaetian age of the Argilliti di Riva di Solto.

SYSTEMATIC

Class	Reptilia Laurenti, 1768
Subclass	Archosauria Cope, 1869
Order	Pterosauria Kaup, 1834
Suborder	Rhamphorhynchoidea Plieninger, 1901
Family	Eudimorphodontiae Wellnhofer, 1978
Genus	*Eudimorphodon* Zambelli, 1973

Type species: *Eudimorphodon ranzii* Zambelli, 1973

Diagnosis: The diagnosis given in 1978 (Wild 1978) must be modified: 5 tarsals (instead of 2); proximal tarsal row consisting of astragalus and calcaneum, distal row of 3 distal tarsals, articulating as a functional unit against proximal tarsal row

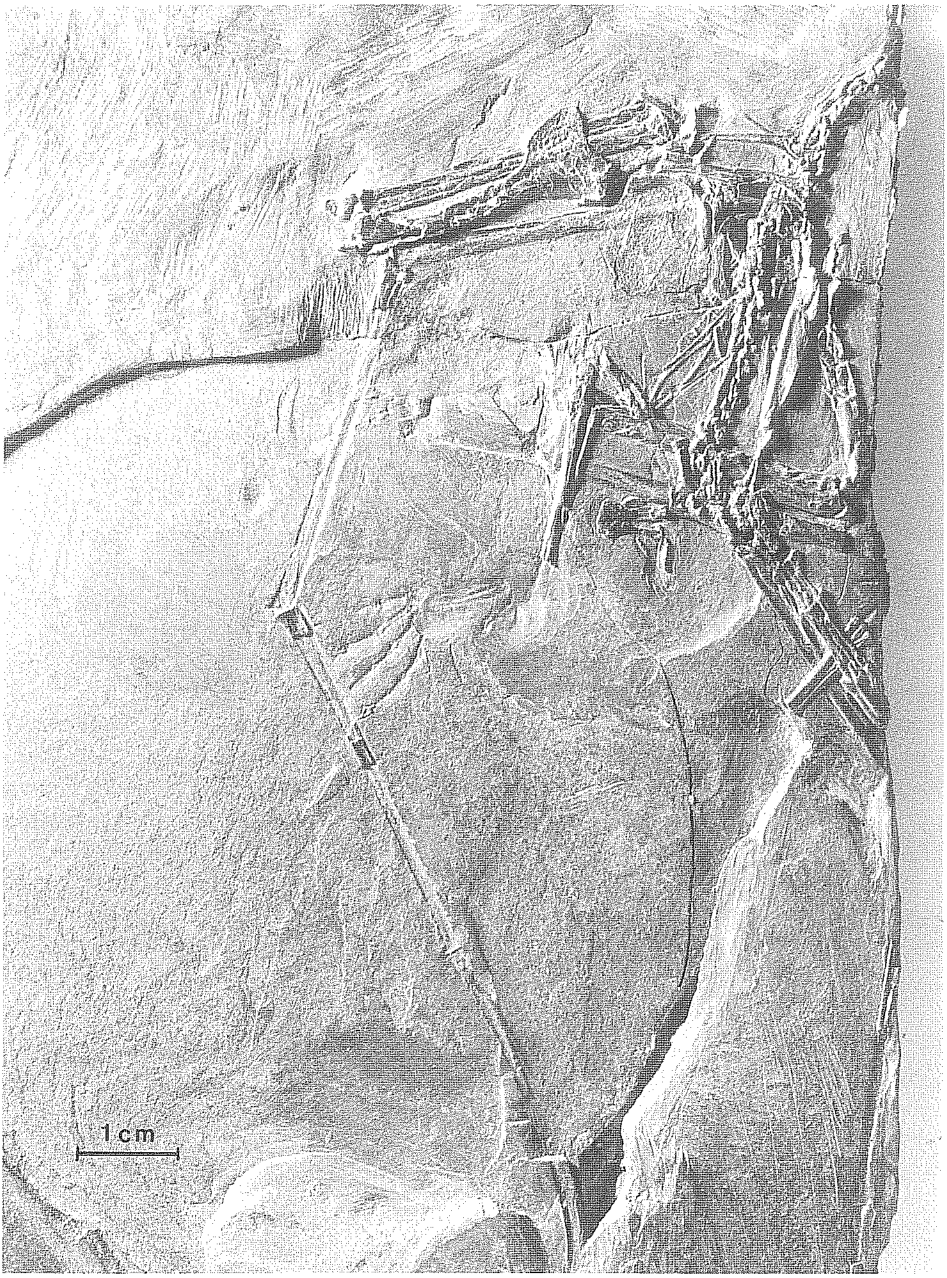

Fig. 1 - *Eudimorphodon ranzii* Zambelli. Photograph of the main slab MCSNB 8950 A.

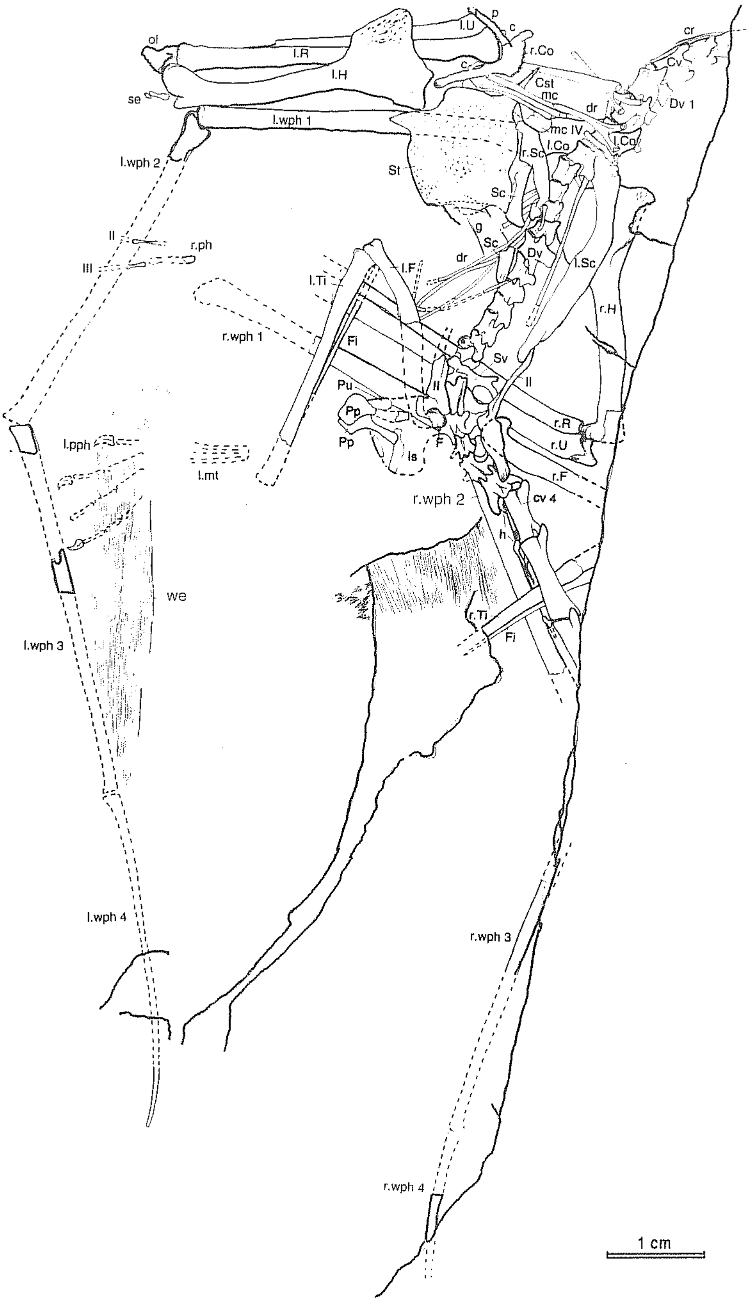

Fig. 2 - *Eudimorphodon ranzii* Zambelli. Drawing of the main slab MCSNB 8950 A; abbreviations: p. 116.

Fig. 3 - *Eudimorphodon ranzii* Zambelli. Photograph of the counter slab MCSNB 8950 B.

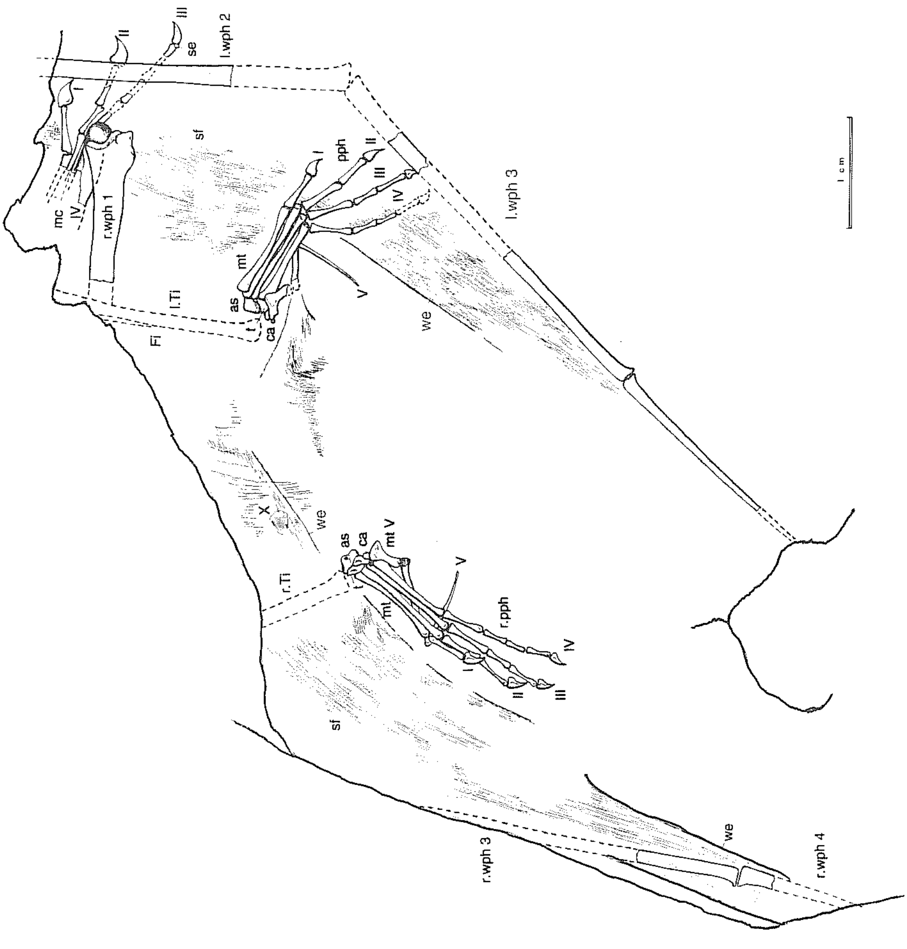

Fig. 4 - *Eudimorphodon ranzii* Zambelli. Drawing of the counter slab MCSNB 8950 B; abbreviations: p. 116; x = enlarged section of figs. 8, 9.

(mesotarsal joint); additional characters and ratios of long bones in MCSNB 8950 are dependent on immaturity (see description).
Distribution: Upper Triassic (Middle Norian), Cene near Bergamo; Upper Triassic (Norian), Ponte Giurino in the Valle Imagna, province of Bergamo, Italy.
Horizon: Lying near the base of the Lower Argilliti di Riva di Solto Formation.
Locality: Ponte Giurino in the Valle Brunone near to the confluence to the Valle Imagna; ca. 500 m northwest of the main church of Ponte Giurino, about 15 km northwest of Bergamo.
Material: MCSNB 8950 A and 8950 B.

DESCRIPTION: The main slab MCSNB 8950 A contains the vertebral column, the shoulder girdle, sternum, pelvis and both wings (Figs. 1,2); on the counter slab MCSNB 8950 B are lying the right metacarpus, and the first 3 fingers with the proximal part of the right first wing phalanx (Figs. 3,4). The skeleton on the main slab is seen from the ventral side. Both slabs show that the pterosaur skeleton was complete and articulated before splitting. The wings are documented by their bones, fragments of the bones or partly their moulds and the wing membranes (Figs. 2,4). The membranes are preserved as a thin film on the dark bituminous shales.
Vertebrae, ribs, haemapophyses and gastrals: The last 3 **cervical vertebrae** (cv) of the vertebral column are preserved together with their elongated **ribs** (cr). They are visible from the left lateral side. The first **dorsal vertebra** (Dv) bears dorsally a slightly forked neural spine which mediates between the low cervical and the high dorsal neural spines. In the middle trunk region the dorsal vertebrae are crushed and/or partly covered by other bones. There are 14 presacral dorsals which are exposed form the ventrolateral side. They are clearly procoelous. The seventh dorsal vertebra is damaged due to the overlying left coracoid, indicating 2 vertebrae instead of actually only one. The last (fourteenth) dorsal vertebra, probably a lumbar one as in the type of *E. ranzii*, is rotated, thus presenting its procoelous vertebral surface. While the first 3 **dorsal ribs** (dr) are still double-headed, the caudally following dorsal ribs are single-headed. They are separated from their corresponding vertebrae which lie nearby. The sacral region of the vertebral column and the pelvis are rotated and are seen from the dorsal side. The 4 **sacral vertebrae** (Sv) are neither fused together nor connected firmly to the ilia. This can be recognized by their slight rotation against each other and by a faint separation from both ilia. Concluding from the firm connection of these bones in the type of *E. ranzii* I interpret this disjunction as a juvenile character.
The **sacral ribs** (sr) are separated from each sacral centrum by a suture (Fig. 5). The first **caudal vertebra** (cv) bears an anteriorly directed pleurapophysis, while in the second caudal vertebra this apophysis is directed posteriolaterally. The third caudal vertebra has almost twice the length of the second, and the fourth measures three times the length of the second. The fifth caudal is incomplete, because of the fracture of the slab. The first **haemapophysis** (h) appears between the second and the third caudal. Between the latter and the fourth caudal the haemapophysis becomes elongated and filifôrm posteriorly, as is known in rhamphorhynchoid pterosaurs (Wellnhofer 1975), while the praezygapophyses and postzygapophyses remain still unelongated. Anteriorly

the second haemapophysis is forked as can be seen in the type of *E. ranzii*. **Gastral ribs** (g) are present; they are disarticulated and dispersed along the trunk.

Shoulder girdle: With the exception of the right **scapula** (Sc) the shoulder girdle is badly crushed. The right scapula, exposed from the medial side, seems to be connected with the right **coracoid** (Co) at an angle of about 90° as in modern birds (Feduccia, 1993: 792). A suture between both right shoulder elements could not be recognized due to the compression of the glenoid region. However, the left scapula and left coracoid are clearly separated; the coracoid is shifted and lies isolated showing its medial side. In contrast to the fused both elements in the type of *E. ranzii* scapula and coracoid are not fused. According to Wellnhofer (1978 a: 13) and Bennett (1993: 94) this points to a juvenile stage.

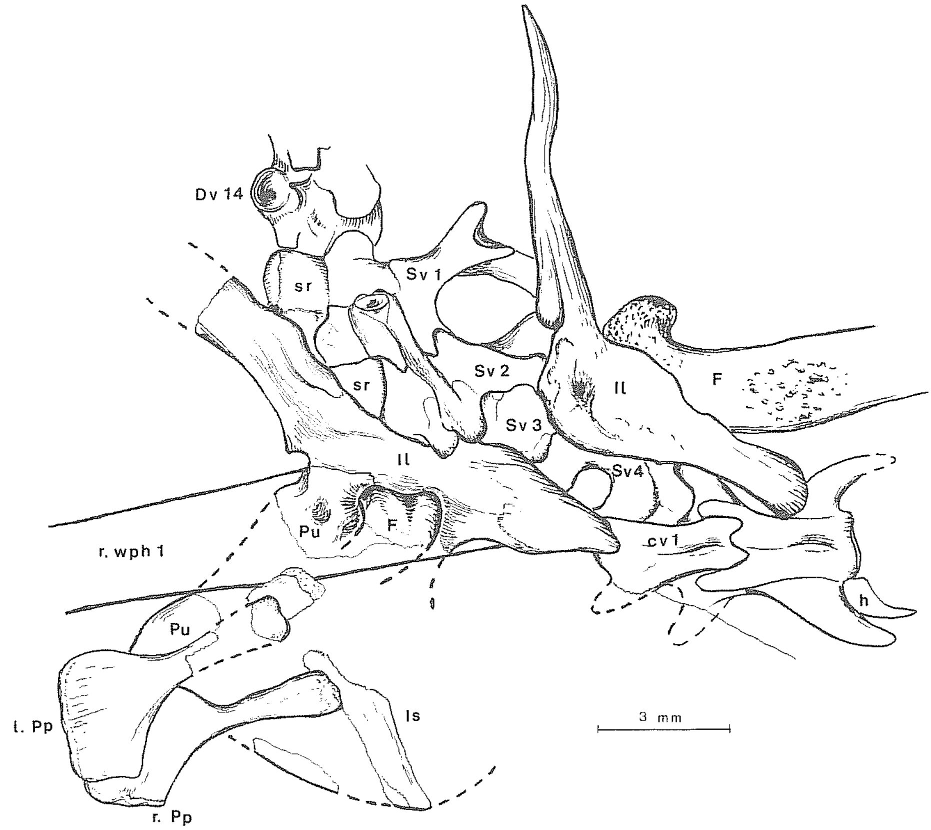

Fig. 5 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 A. Drawing of the pelvis and sacral region; abbreviations p. 116.

Sternum (Fig. 6): The large quadrangular sternum is seen from the dorsal side. It reveals a tripartite configuration of the plate: both lateral areas and the medial part present a fine granulated bone surface while both the enclosed areas of the plate are smoothly structured. This different structure of the sternum is clearly visible as colour differences of the corresponding areas after using the solvent acetone. These different structured areas are attributed to different bone tissues and are probably of different origin. Either each lateral part of the plate represents a single sternal element or each intercalated smoothly structured area has its independent sternal origin. The tripartite configuration of the sternum points to a heterogenous development of this bone during ontogeny. It could only be recognized by the immaturity of this pterosaur and the rare presentation of the dorsal view of the sternum. The ontogenetic development of the sternum in MCSNB 8950 of *E. ranzii* has a parallel in the ontogenetic growth of the sternum in eosuchians: In the Permian *Youngina* (Broom 1922), *Thadeosaurus* (Carroll 1981), *Hovasaurus* (Currie 1981), the Early Triassic *Kenyasaurus* (Harris & Carroll 1977) and the Upper Permian palinguanids as descendents of the eosuchians (Haughton 1929; Carroll 1975, 1977). Also in recent lacertilians a paired "Anlage" of cartilaginous sternal elements reflects the eosuchian condition. The sternum of MCSNB 8950 reveals another morphological feature which may be of interest for the development of this plate: The anterior border of the plate is buttress-like strengthened and seems to consist of two medially contacting and partly overlapping elements, which are firmly fused to the sternal plate, similar as described and figured by Currie (1981: 140 f.; fig. 20) in *Hovasaurus*. This anterior buttress is supposed to have been developed by the clavicles, marked "Cl" in Fig. 6b. If this interpretation is correct, the medial cristaspina sterni connected to both clavicles and elongated in the medial stem of the sternal plate represents the interclavicle ("ICl" in Fig. 6b). The sternum of MCSNB 8950 most likely has a multipartite origin of different elements which fuse to a single uniform bony plate during ontogeny. The sternum of *Eudimorphodon* and perhaps also of all other pterosaurs, seems to be a neomorphous bone, which is not homologous to that of birds.

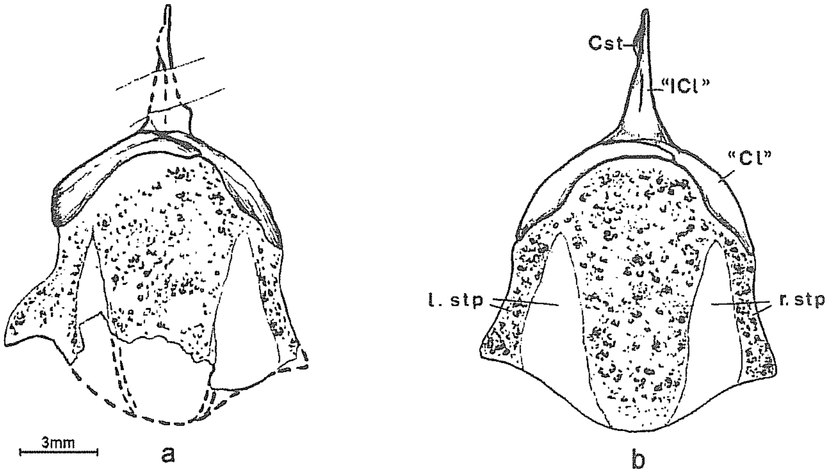

Fig. 6 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 A . Drawing of the sternum, a = as preserved, b = reconstructed; abbreviations: p. 116.

Right wing (Fig. 4): The right wing is seen from the ventral side. The right **humerus** (H) is still articulated in the glenoid cavity of the scapula and coracoid. It is badly crushed. In the elbow joint the lower arm with **ulna** (U) and **radius** (R) is bent backwards, about 90° anterioproximally. The radius is slightly shifted distally due to the partly preserved condylus radialis of the humerus in the way as described in other pterosaurs (Wellnhofer 1987 a: 17). Both distal ends of ulna and radius are broken off and have been lost with the adjacent slab. Because the right wing is still in its natural articulation, and based on the drawings (Figs. 2,4), the length of the lower arm can be taken from the counter slab MCSNB 8950 B. The moulds of the **carpals** (c) are visible near the fracture of the slab pointing to at least 3 larger carpals: A large proximal one and 2 distal ones. Distally of the carpals one can see the moulds of the **metacarpals I-III** (mc I-III). Their distal ends are preserved in bone. The first 3 **fingers** (ph I-III) of the manus bear strong hooked claws. The latter have almost twice the size of the claws of the pes. At the extension side of the third finger, between the third phalanx and the following claw, a tiny **sesamoid bone** (se) is situated. Close to the distal end of the **wing metacarpal** (mc IV) the posterioventrally projecting crista metacarpi for the origin of the flexor muscle of the wing finger is seen. The wing metacarpal contacts the **first wing phalanx** (wph 1) with its trochlea metacarpi. The latter is extremely bent backwards lying parallel to the lower arm. The anterior situated roughly structured olecranon-like process of the first wing phalanx corresponds to that one of the Milano specimen of *E. ranzii*. The **second, third and fourth wing phalanges** (wph 2, 3, 4) are preserved mainly as moulds. In this region of the wing spar remains of the wing membrane can be identified. The wing membrane runs from posterioproximal to anteriodistal. It is crossed by the twisted wing spar between third and fourth wing phalanx (Fig. 4): The wing tip exposes its dorsal surface; proximal of the third wing phalanx the wing membrane is seen from its ventral surface.

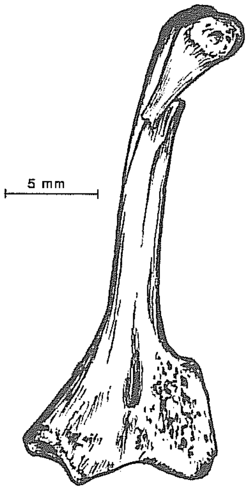

Fig. 7 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 A. Drawing of the left humerus.

Left wing (Figs. 2,4): The left **humerus** (H) is separated from the scapula and coracoid, rotated and exposed from the dorsal side. The humerus is well ossified compared with that one of the Milano specimen of *E. ranzii*, which is about of the same size (Figs. 7,14). The deltopectoral crest for the attachment of the pectoralis - and deltoideus- musculature resembles that of the type of *E ranzii*. The slightly concave articulation facet of the caput humeri is saddle-shaped and proximodorsally surrounded by a bony bulge. The shaft of the humerus is crushed; the distal end with the anteriodorsally directed trochlea is well ossified. The left lower arm is almost naturally connected to the humerus. It is crushed, twisted and therefore visible from the radial side. The left **radius** (R) is overlying the left **ulna** (U). Both bones are bent backwards about 320°. The ulna exposes its oblique, saddle-shaped proximal articulation cavity from the ventral side. This cavity is surrounded by knobs and continues into the **olecranon** (ol). Movements of the lower arm against the humerus are therefore restricted mainly in anterior-posterior direction. Near the condylus ulnaris of the humerus lies a small, slightly bent, rod-like bone (Fig. 2) which could be a **sesamoid bone** (se). Near this bone lies another 0.45 cm long, lens-shaped bone. I consider it to be also a **sesamoid bone** (se) of the lower arm extensor muscles or their tendons (Fig. 4). These sesamoids are reported here for the first time for pterosaurs. The carpus of the left manus is partly disarticulated and the **carpals** (c) are superimposed by the right coracoid. The right **pteroid** (P), partly covered by the right coracoid, is twisted against the carpus and points posteriorly. Its proximoanterior end is broken off. In its shape the pteroid of MCSNB 8950 resembles that of MCSNB 2887 of *E. ranzii*, described 1978. The first 3 **metacarpals** (mc I-III) are twisted against the wing metacarpal. Their distal ends are covered by the right coracoid. The first 3 **fingers** of the manus (ph I-III) are hidden under the right coracoid and vertebral column. The **wing metacarpal** (mc IV) articulates with the **first wing phalanx** (wph 1). Although both bones are covered by the overlying sternum their shape can be recognized below that bone so that measurements can be taken (Tab. 1). The distal end of the first wing phalanx is contacting the **second wing phalanx** (wph 2), which is rotated and presents its posterior side. Its proximal end exibits a distinct saddle-shaped articulation facet, which would allow only little movement of this wing phalanx in anterior-posterior direction. This could neither be observed in the type nor in the Milano specimen of *E. ranzii*. However, it was recognized in *Peteinosaurus zambellii* (Wild 1978: 230; Fig. 39). The second wing phalanx and **third wing phalanx** (Wph 3) are preserved only by their proximal ends and by a fragment of the shaft region or by their moulds. The **fourth wing phalanx** (wph 4) is documented in the same way. There are preserved fossil remains of the left wing membrane, too.

Wing membrane: MCSNB 8950, mentioned by Padian & Rayner (1993: 97; tab. 1) under n° 1431 (provisional stratigraphic number), is the first Triassic pterosaur with fossil remains of the wing membrane. The membrane is attached to the wing finger spar and extends from the trunk region until the tip of the fourth wing phalanx. Although partly destroyed by the first provisional preparation (subparallel scratches; figs. 1, 3) it can be seen mainly between the second and fourth wing phalanges (Figs. 2, 4). The membrane of both wings is folded and crossed in the region of the first and second wing phalanges due to the postmortal flexion of the wing finger. Additionally,

Fig. 8 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 B. Photograph of the section from the right wing membrane, marked x in Fig. 4.

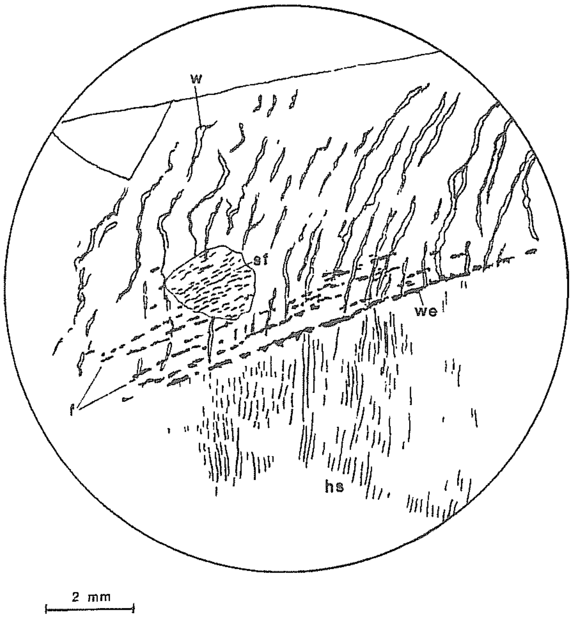

Fig. 9 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 B. Drawing of the section from the right wing membrane of Fig. 8; abbreviations: p. 116.

the distal end of the right membrane crosses the wing spar between the third and the fourth wing phalanx. It exposes its dorsal surface while the proximally following part of the membrane presents its ventral surface. At both membranes the **posterior trailing edge** (we) is strengthened and obviously stiffened by a black "carbonized?", about 0.1 mm thick strip (Figs. 8-10). This observation supports Pennycuick's (1986; 1988: 309 ff., 1990) statement that the trailing edge was stiffened by a tendon, which ran from the tip of the wing to the posterior trunk region or fifth toe. It seems to be most probable that the membrane with its reinforced trailing edge was attached to the fifth toe in *Eudimorphodon* (Fig. 4, 8). This assumption would contradict my opinion (Wild 1978) and the observation of Padian & Rayner (1993) that the membrane did only reach the trunk.

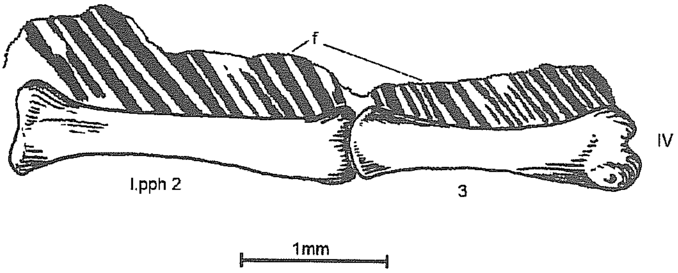

Fig.10 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 B. Drawing of a small section from the left wing membrane, from dorsal, preserved by the overlying foot; the zebra-like stripes are folds and/or partly structural fibres (which are covered by the overlying parallel running folds); abbreviations: p. 116.

The most remarkable features of the membrane are the **structural fibers** (sf) (Padian & Rayner 1993; "Aktinofibrillen" after Wellnhofer 1987 b). In the region of the first wing phalanx these structural fibers originate almost vertically from the wing finger spar and reach the trailing edge of the membrane under a right angle. Further distally, and to the tip of the wing, the fibers build an acute angle or run parallel to the wing spar or trailing edge. They are lying on the ventral surface of the membrane, as stated by Wellnhofer (1987 b) and Padian & Rayner (1993) in Upper Jurassic pterosaurs. The angle between the fibers and the wing spar and that to the posterior edge of the membrane depends on the structure, folding and crossing of the membrane (Figs. 8, 9). The fibers and their orientation are well known from many Upper Jurassic pterosaurs. They are not wrinkles as they were interpreted by Pennycuick (1986, 1988). The length of the fibers is difficult to determine since they are paralleled by folds (Figs. 8, 9; see below) or are visible as thin, black, "carbonized ?", very short striae, similar to a broken line. Their width is rather variable: Nearby the wing spar they are 0.01- 0.02 mm thick, whereas the width increases towards the trailing edge of the wing membrane to 0.05 and 0.1 mm. The distance between the fibers depends on the stretching of the patagium. It ranges from anterior to posterior between 0.05 and 0.15 mm. These measurements correspond to those in *Pterodactylus* and *Rhamphorhynchus* (Wellnhofer 1975; 1987 b; Padian & Rayner 1993). The length of the fibers is related to the stiffness of the wing membrane (Padian & Rayner 1993: 126). Elongate fibers indicate a stiff membrane, whereas short fibers are more likely associated with a soft wing. It is not the shape of the wing membrane and its supposed attachment to the legs (Unwin 1992) or body (Padian 1979; Padian & Rayner 1993) that influences the stability of the membrane in pterosaurs, but the length and arrangement of these fibers (Unwin & al. 1993). The proximal part of the wing in pterosaurs has very short fibers, which diminish and disappear towards the body. Therefore Martill & Unwin (1989) could not recognize fibers near the lower arm in the described wing section of the Cretaceous pterosaur. In the proximal part of the flexed lower arm of MCSNB 8950, in the region of wing metacarpal and first wing phalanx, lies the main folding region of the wing. There the membrane is folded, crossed, sometimes covered by its own parts or is torn. The structural fibers follow the flexed wing and are curved without becoming broken (Fig. 11). These observations are also made by Wellnhofer (1975) and Padian (1983) and contradict Pennycuick's (1986, 1988) view. Proximal near the trunk region the structural fibers as group of stripes are oriented obliquely towards each other, caused by the disruption of the patagium during decay or fossilization. Or they cross in bundles, caused by the folding of the membrane, as described by Leich (1964) in *Rhamphorhynchus*.

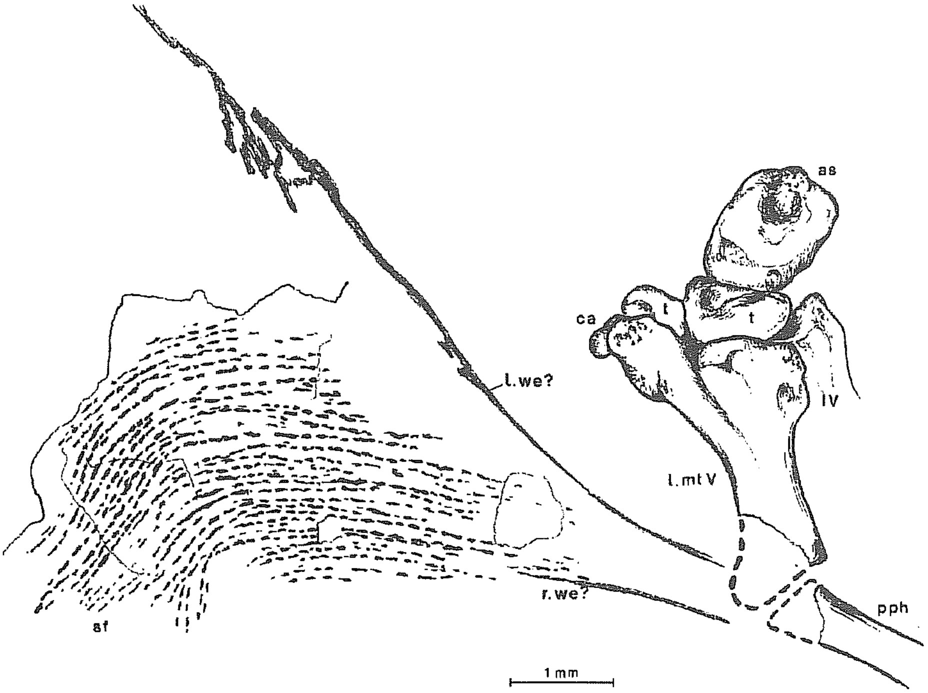

Fig.11 - *Eudimorphodon ranzii* Zambelli; MCSNB 8950 B. Drawing of a section of the right wing membrane with curved structural fibers; abbreviations: p. 116.

In the proximal part of the wing in MCSNB 8950 also **wrinkles** (w) appear, which are not observed in the distal part of the membrane. These true wrinkles are arranged more or less vertical to the trailing edge of the membrane (Figs. 8, 9). They do not correspond to wrinkles as defined by Pennycuick (1986, 1988, 1990). I suppose (see above) they appear in groups or singly and run in an undulating fashion. Their distance from each other, if arranged in groups, varies from 0.3 to 1.5 mm.

There can be seen also **folds** (f) running parallel to the structural fibers and towards the tip of the wing (Figs. 8-10). They appear as black, 0.1 mm thick stripes on the dorsal surface of the wing membrane, arranged sometimes in a zebra-like pattern (Fig. 10). Paralleling the fibers, they are covering the latter. Sometimes it is difficult to distinguish between folds and fibers if the wing membrane is preserved on both split slabs.

In the described specimen MCSNB 8950 of *E. ranzii*, **hair-like structures** (hs) are present on the wing membrane, however, only in the region between humerus and lower arm and between first and second wing phalanx (Figs. 8, 9). This corresponds to the observation in *Rhamphorhynchus* made by Broili (1927: 54; Taf. 4; 7, fig. 1). These are very thin 0.01 to 0.02 mm thick, parallelly oriented striae, separated by distances of 0.08 to 0.1 mm. Their average length is about 0.4 mm. Broili (1927, 1938) describes them as tiny, densely but irregularly grouped needle-pointed grooves in *Rhamphorhynchus* and *Pterodactylus*. The preservation of these hair-like structures seem to be different in the plated limestones of Solnhofen-Eichstätt and in bituminous shales. In *Dorygnathus* (Broili 1939) they are preserved three dimensionally as is the case in the described specimen of *E. ranzii*, MCSNB 8950. In the Solnhofen limestones they are preserved as moulds by dissolution of their organic material. Nothing can be seen of hair-like structures or even a "fur" in the body region of MCSNB 8950, compared with *Dorygnathus* (Broili 1939: 131). If present they were lost during preparation process.

Pelvis girdle (Fig.5): The pelvis girdle, exposed from the ventral side, is incompletely preserved and additionally crushed. By splitting the slab, the right pubis and the right ischium broke off and were almost completely lost. The **ilium** (Il) has an elongate praeacetabular, spatula-like process; the one of the right side is broken off anteriorly. The postacetabular process can be clearly seen at the left half of the pelvis and corresponds to that of *E. ranzii* (Wild 1978: 213; fig. 21). The **pubis** (Pu), preserved only with its acetabular part on the left half of the pelvis, is connected to the ilium by a suture (Fig. 5). At the suture between ilium and pubis the left ischium is broken off. A distal fragment marks the anterioventral border of the plate. Both acetabula have still articulating femora (Fig. 5), and both praepubes lie near the pelvis. The quadrangular shape of the **praepubis** (Pp) differs from the leaf-like shape of the type of *E. ranzii* (Figs. 5, 16); furthermore the stem for attachment to the pubis is longer. This is due to ontogenetic changes during growth. The praepubis of MCSNB 8950 resembles that of *Dorygnathus* (Arthaber 1919: 59 ff.; fig. 41) and *Campylognathoides liasicus* (Quenstedt) (Wellnhofer 1974: 20 f.; fig. 9).

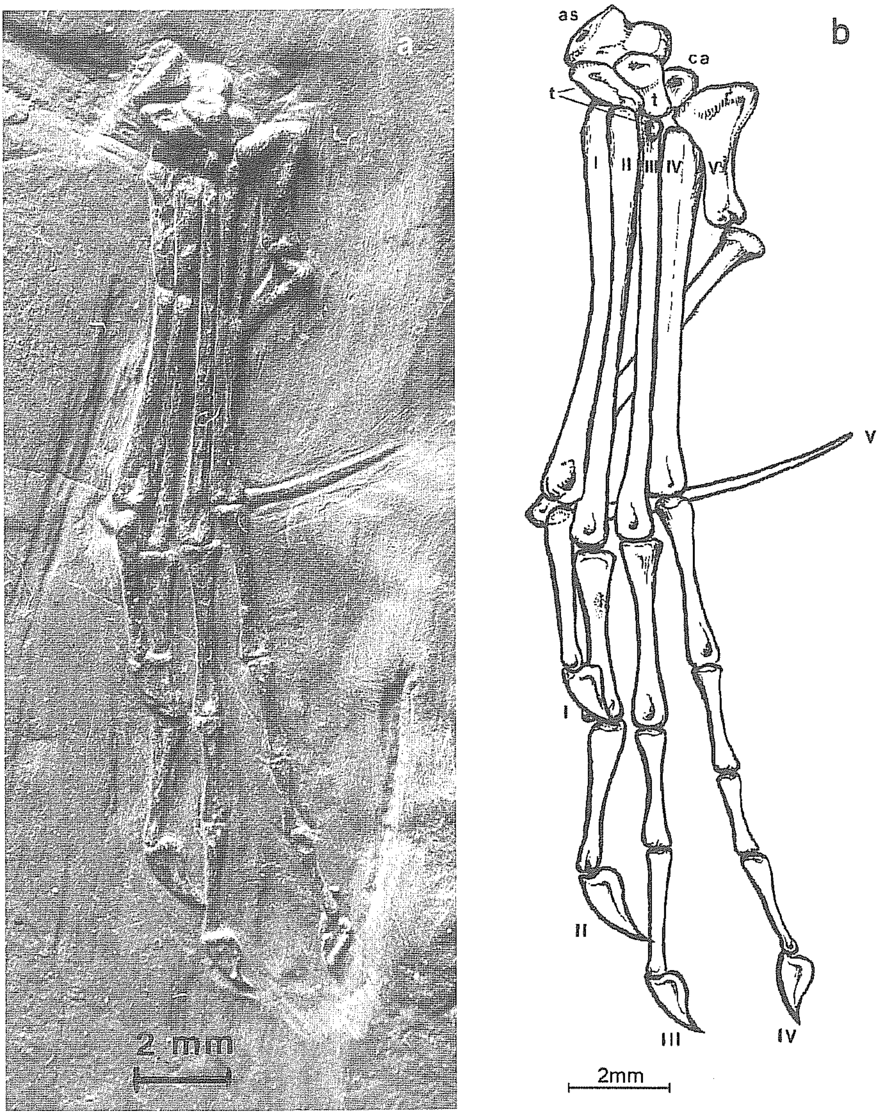

Fig.12 - (a) *Eudimorphodon ranzii* Zambelli; MCSNB 8950 A. Photograph of the right foot. (b) *Eudimorphodon ranzii* Zambelli; MCSNB 8950 A. Drawing of the right foot; abbreviations: p. 116.

Posterior limb (Figs. 12): Both posterior limbs are preserved incompletely, but can be reconstructed by combining slab and counter slab. Both femora are articulated to the pelvis; the right **femur** (F) is preserved in its proximal part, while the left femur is represented by the middle part of the shaft and by the caput femoris, which is articulated in the left acetabulum. Its distal condyle is damaged. However, the femur can be reconstructed by combining bone fragments with the moulds on slab and counter slab; thus, its length can be determined (Tab. 1). **Tibia** (Ti) and **fibula** (Fi) are incompletely preserved or partly as moulds on both slabs. They are unfused. This is another feature that indicates immaturity. The length of the fibula is about 2/3 of the tibia. The right tibia and fibula are lying in natural position with respect to femur and ankle (Figs. 2, 4). On the counter slab MCSNB 8950 B both feet are articulated and seen from the ventral side (Figs. 12). The **tarsus** consists of 5 elements: the **astragalus** (as), proximally ending in a double groove for the articulation with the tibia and the **calcaneum** (ca); both these tarsals are arranged in the proximal tarsal row; 2 **distal tarsals** and a very small slightly disarticulated **lateral distal tarsal** (t) near the proximal end of the metatarsal IV are lying in the distal tarsal row (Figs. 11-12). These 3 distal tarsals fit together and seem to have been articulated as a functional unit, building a mesotarsal joint. The tarsus resembles that of *Peteinosaurus zambellii* Wild (loc.cit.; p.232; fig. 41) but differs from that in *E. ranzii* (loc.cit.; p.214 f.). This may be due to its incompleteness of the tarsus of all *Eudimorphodon* specimens known so far. **Metatarsals I-IV** (mt I-IV) are of about the same length. Proximally they overlap each other from medioventrally to laterodorsally and hence must have functioned as a unit. The **metatarsal V** (mt V) is a very short but stout and proximally enlarged bone. Its distal end carries a hemispherical articulation knob, which enables the **first phalanx** (pph 1) of the fifth toe to move in nearly all directions (comparable to that of *P. zambellii*; figs. 11-12). in the middle of the shaft of the metatarsal V a knob, the tuber metatarsi, serves for the insertion of a muscle for opposable movements of the **fifth toe** (pph V). This can be interpreted as in *P. zambellii*: The fifth toe may serve for spanning and directing a web between the toes. However, it must be taken into consideration that the fifth toe may have spanned the enlarged uropatagial part of the wing membrane. The claws of the pes are much shorter, smaller and less curved than those of the manus. This points more to ground-dwelling than to climbing or perching, as would be the case for *Archaeopteryx* and modern birds (Feduccia 1993: 792; fig.6). The phalangeal formula of the pes is: 2 3 4 5 2 as in most pterosaurs (Fig.12).

COMPARISON: The new pterosaur specimen MCSNB 8950 belongs to the genus *Eudimorphodon* based on the characteristic shape of the humerus (Fig.13), the shield-like sternum (Fig. 14) and the proportions of the skeletal bones (Tab.2). However, there arises the question whether the new find is a juvenile specimen of *E. ranzii* or if it represents a small-sized new species of *Eudimorphodon.*

Although the new specimen lacks the skull, and therefore such important diagnostic features as the dentition is unknown, there are some characters to define its ontogenetic age and/or specific status. MCSNB 8950 is of almost the same size as the Milano specimen of *E. ranzii* (Tab.1). The latter specimen is badly preserved; most of the long bones are documented by their moulds. Some bones seem to be incompletely ossified, mainly on their epiphyses. In contrast to the Milano specimen, nearly all bones of MCSNB 8950 are well ossified. Nevertheless I regard MCSNB 8950 as an immature specimen of *Eudimorphodon* on account of the following characters: Sternum incompletely ossified, without processi for the attachment of the sternocostal ribs (Fig.14); no sternocostal ribs preserved; scapula and coracoid separated (Fig.2); sacral

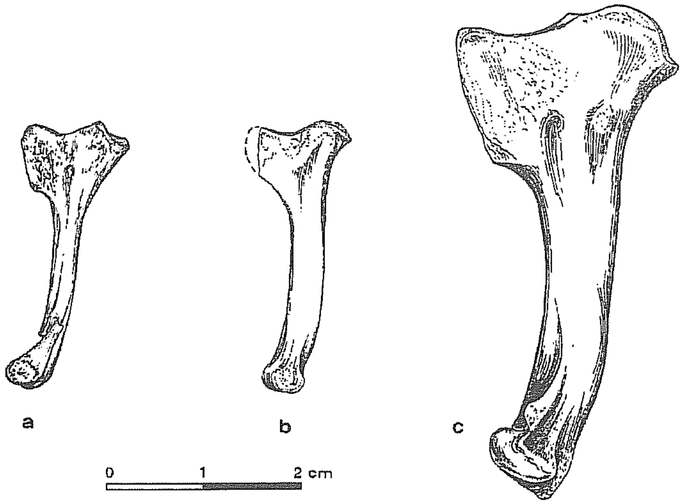

Fig.13 - *Eudimorphodon ranzii* Zambelli. Left humerus of juvenile specimens (a, b) and adult specimen (c) in dorsal view illustrating the morphological and proportional change during ontogeny; a = MCSNB 8950 A, b = Milano specimen, c = MCSNB 2888 (after Wild 1978).

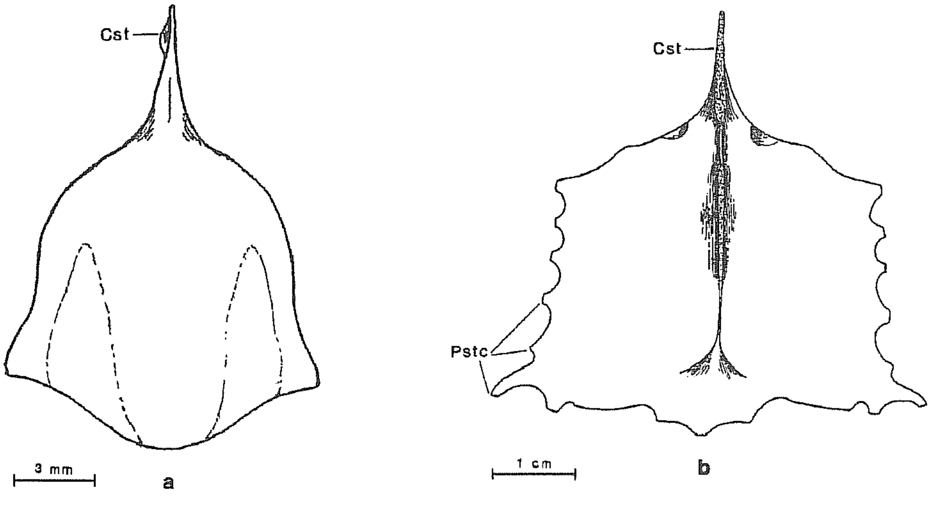

Fig.14 - *Eudimorphodon ranzii* Zambelli. Drawing of reconstructed sternum illustrating the morphological change during ontogeny; a = juvenile specimen MCSNB 8950 A, b = adult specimen MCSNB 2888 (after Wild 1978); abbreviations: p. 116.

ribs not fused to the centra and separated from the ilia by sutures (Fig.5); ilium and pubis separated by a suture (Fig.5); tibia and fibula unfused; however, this feature does not consequently point to immaturity according to Wellnhofer (1987 a) (Fig.2).

	Type of *E. ranzii*	Milano specimen	MCSNB 8950
H	47	26	26
U	65	35	33,5
mcIV	29	9,8	9,3
wph1	80*	38,5	33
wph2	-	33*	35
wph3	-	36	35,5
wph4	-	35*	32
F	41	19*	19,6
Ti	50*	25*	25,5

Tab.1 Length (in mm) of postcranial bones of *Eudimorphodon ranzii* Zambelli, type (MCSNB 2888), and immature specimens (Milano specimen and MCSNB 8950). * = approximated; abbreviations: p. 116

	Type of *E. ranzii*	Milano specimen	MCSNB 8950	MCSNB 2887
U/H	1,38	1,35	1,29	1,36
H/mcIV	1,62	2,65	2,80	2,00
U/mcIV	2,24	3,57	3,60	2,27
H/F	1,15	1,37	1,33	1,27
H/Ti	0,94*	1,04*	1,02	0,98
U/F	1,59	1,84	1,71	1,72
U/Ti	1,3*	1,4*	1,31	1,33
Ti/F	1,22*	1,32*	1,30	1,29
F/mcIV	1,41	1,94*	2,11	1,57
Ti/mcIV	1,72	2,55*	2,74	2,03
wph1/H	1,7*	1,48	1,27	1,41
wph1/U	1,23*	1,10	0,99	1,04
wph1/mcIV	2,76*	3,93	3,54	2,82
wph1/F	1,95*	2,03*	1,68	1,80
wph1/Ti	1,6*	1,54*	1,29	1,39
wph2/wph1	-	0,86*	1,06	1,01*
wphl3/wphl2	-	1,09*	1,01	-

Tab.2 Ratios of postcranial bones of *Eudimorphodon ranzii* Zambelli, type (MCSNB 2888), subadult specimen (MCSNB 2887) and immature specimens (Milano specimen and MCSNB 8950). * = approximated; abbreviations: p. 116

The ratios of the postcranial bones of MCSNB 8950 correspond with those of the Milano specimen of *E. ranzii*. MCSNB 8950 differs in the proportion of the first and the second wing phalanx from the type and to a lesser degree from the Milano specimen and the subadult specimen MCSNB 2887. The first wing phalanx is a little shorter than the ulna; the second wing phalanx is longer than the first wing phalanx. In all other specimens of *E. ranzii* this proportion is reverse: the first wing phalanx is a little longer than the ulna, and the second wing phalanx is shorter than the first wing phalanx. This ratio is only a useful character to define pterosaur species or genera (Wellnhofer 1974; Wild 1984) if it is supported by other distinctive ratios. This is not the case in MCSNB 8950. The ratios between second and first wing phalanges and first wing phalanx to ulna vary during ontogeny, as can be seen in tab.2. In MCSNB 2887 the first wing phalanx has about the length of the second (Wild 1978: 241; tab.6); it is intermediate between the juvenile and adult (MCSNB 2888) specimen. So the ratios referring to the first 2 wing phalanges and the ulna do not justify the erection of a new species for MCSNB 8950. The different ratios of the first 2 wing phalanges and the ulna are due to the intraspecific variability during growth. There seem to be differences in the structure of the distal end of the tibia and ankle in MCSNB 8950 and the known specimen of *E. ranzii* with regard to the development of a distal trochlea at the tibia and the number of the tarsals (Figs.4, 12). As is shown in the descriptive part, however, I had to correct the number of tarsals in *Eudimorphodon* from 2 to 5, since the type of *E. ranzii* and the other described specimens are incompletely preserved in the ankle region.

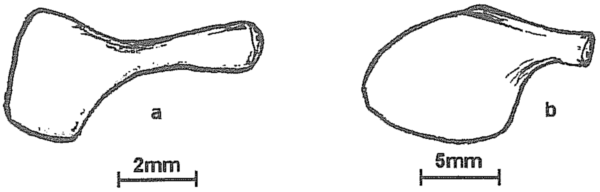

Fig.15 - *Eudimorphodon ranzii* Zambelli. Drawing of the right praepubis illustrating the morphological change during ontogeny; a = juvenile specimen MCSNB 8950 A, b = adult specimen MCSNB 2888 (after Wild 1978).

Another difference between MCSNB 8950 and the type of *E. ranzii* refers to the praepubis (Fig.15). Whereas it is leaf-shaped and supported by a short pubic process in the type, it is hatched-shaped in MCSNB 8950. I consider these morphological changes of the praepubis in *E. ranzii* as related to growth during ontogeny.

Finally the pteroid is also influenced by ontogenetic changes during growth. It is hatched-shaped in the type and MCSNB 2887 of *E. ranzii*, rod-like in the Milano specimen and intermediate in MCSNB 8959.

ABBREVIATIONS

MCSNB	Museo Civico di Scienze Naturali "E.Caffi" Bergamo
as	astragalus
c	carpal
ca	calcaneum
Cl	clavicle
Co	coracoid
cr	cervical rib
Cst	cristasspina sterni
Cv	cervical vertebra
cv	caudal vertebra
dr	dorsal rib
Dv	dorsal vertebra
F	femur
f	fold
Fi	fibula
g	gastral rib
H	humerus
h	haemapophysis
hs	hair-like structures
ICl	interclavicle
Il	ilium
Is	ischium
l.	left
mc	metacarpal
mt	metatarsal
ol	olecranon
P	pteroid
ph	phalanx of manus
Pp	praepubis
pph	phalanx of pes
Pstc	sternocostal process
Pu	pubis
R	radius
r.	right
Sc	scapula
se	sesamoid bone
sf	structural fibers
sr	sacral rib
St	sternum
stp	sternal plate
Sv	sacral vertebra
t	tarsal
Ti	tibia
U	ulna
W	wrinkle
we	wing edge
wph	wing phalanx

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