REDESCRIPTION OF *TRIADOBATRACHUS MASSINOTI* (PIVETEAU, 1936) AN ANURAN AMPHIBIAN FROM THE EARLY TRIASSIC

BY

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With 5 figures in the text

Zusammenfassung

Triadobatrachus massinoti, ein Lurch aus der älteren Trias Madagaskars, wird auf Grund eines sehr genauen Silikonabgusses des Typus-Exemplares, das als natürlicher Abguß erhalten ist, erneut beschrieben.

Im Gegensatz zu den früheren Beschreibungen kann man vor allem feststellen, daß das Frontoparietale nicht unpaar ist, das Schädeldach lateral zwei paarige Knochen enthält (wahrscheinlich das Nasale und einen anderen Knochen, der entweder das Praefrontale, das Lacrimale oder der Processus frontalis maxillae sein kann), und weiter, daß das Palatinum, das sich bei dem Fossil in der Orbita befindet, in sie verlagert wurde. Das Quadratojugale fehlt, und die dritte Rippe ist nicht seitlich gegabelt. Überdies ist das Opisthoticum und auch das Occipitale laterale vorhanden, jedoch fehlt das Operculum. Zähne sind nicht erhalten. Die Wirbelgelenke sind amphicoel, möglicherweise mit Ausnahme jenes zwischen dem Atlas und dem 2. Wirbel, das opisthocoel sein könnte. Das Zentrum des Atlas ist aus zwei ossifizierten Teilen (anterioren und posterioren) gebildet. Der Atlas trägt zweiköpfige Rippen, während alle anderen Rippen einköpfig sind. Sechs Schwanzwirbel sind sichtbar, aber der Schwanz war wahrscheinlich länger. Die Rippen waren möglicherweise an allen Schwanzwirbeln ausgebildet.

Triadobatrachus massinoti ist keine Larve. Er stellt ein Individuum dar, das nach der Metamorphose jedoch noch nicht völlig ausgewachsen war. Er weist einige fortgeschrittene Züge auf, die für Proanura charakteristisch sind. Diese Merkmale schließen hauptsächlich die Schädelstrukturen ein, während das Postkranialskelett mehr dem generalisierten Typus angehört, mit einer Ausnahme des Beckengürtels, der mehr an moderne Anuren erinnert.

Triadobatrachus massinoti ist eng mit einem Froschvorläufer verwandt, aber seine Beziehungen zu anderen Froschgruppen bleiben unbekannt. Trotz dieser Verwandtschaftsverhältnisse war *Triadobatrachus* noch nicht springfähig. Deswegen kann die Adaptation zum Springen nicht als Anlaß zur Entstehung der Frösche gewertet werden.

Schlüsselwörter: Amphibia — Anura — Evolution — Trias.

Abstract

Triadobatrachus massinoti, an amphibian from the early Triassic of Madagascar, is redescribed on the basis of high resolution silicon rubber casts made from the type-specimen which is preserved as a natural mold.

Contrary to various previous descriptions, it may be mainly established that the frontoparietal is not azygous, the skull roof anteriorly retains two paired bones (probably a nasal and another bone that could be either a praefrontal, a lacrimal or the frontal process of the maxilla),

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the palatine that is exposed in the orbit has been displaced, the quadratojugal is lacking and the third ribs are not bifurcate laterally. Moreover, both opisthotic and lateral occipital are present but an operculum is lacking. No tooth is discernible. The vertebral joints are amphicoelous, excepting perhaps the atlas/second vertebra joint that could be opisthocoelous. The atlantal centrum is made of two (anterior and posterior) ossified parts. The atlas bears double-headed ribs, the other ones being single headed. Six caudal vertebrae are exposed but the tail was probably longer; ribs were perhaps present on all caudal vertebrae. *Triadobatrachus* is not a larva; it corresponds to a post-metamorphosed, but not yet fully matured individual. It displays some advanced features that are characteristics of anurans; these advanced characteristics chiefly concern skull structures whereas post-cranial skeleton is of a generalized type, except the pelvic girdle which heralds that of modern anurans.

Triadobatrachus is closely related to the anuran ancestor but its relationships with other amphibians remain unknown. Despite these relationships, *Triadobatrachus* was not yet capable of effective jump; therefore saltatorial adaptation was not the impetus of anuran origin.

Key words: Amphibia — Anura — evolution — Triassic.

Contents

Introduction

In our preliminary report (RAGE & ROČEK 1986), it was stated that *Triadobatrachus massinoti* (PIVETEAU 1936), a unique early Triassic fossil amphibian known already more than fifty years ago by only a single specimen found in Northern Madagascar, is not yet satisfactorily interpreted both from the view of its phylogenetic position and its individual age.

This holds true despite of some more or less extensive discussions, most of them, however, being founded on brief observations of the holotype or based on figures and old casts only. Moreover, taking over information from earlier publications led to some misinterpretations and incorrectnesses that have subsequently tended to spread into general paleontological literature. As the notes on *Triadobatrachus*, commonly regarded as an intermediate between primitive amphibians and anurans, are often included into large compendia on vertebrate paleontology (e. g. ROMER 1966) or text-books dealing with the evolution of vertebrates (e. g. McFARLAND et al. 1979), there appeared a need for accurate description and illustrations of the fossil, as well as for its correct restoration. For this reason we decided to make a new investigation based on high resolution casts made of silicon rubber, and to check all published data in order to point out all of them which are incorrect. In the descriptive part, special attention will be given only to those structures that were misinterpreted or have not been reported at all; those which are interpreted in accordance with earlier authors are only referred to the pertinent literature.

Acknowledgements

Geographic and stratigraphic occurrence

The taxon is based on a natural mold enclosed in a nodule. The mold does not lie entirely in the nodule: the anteriormost part of the skull, the two manus and parts of hind limbs are lacking (Text-fig. 1). They have been either worn away by the erosion or, perhaps, have never been included within it. Each intersection of the mold with the surface of the nodule corresponds to a hole that connects the internal mold with the outside.

The nodule was found near Betsieka (a village in Northern Madagascar) by an amateur, A. MASSINOT, who gave it to J. PIVETEAU. It comes from shales that have yielded numerous fishes (also enclosed in nodules), ammonites, other amphibians and some plant fragments (BESAIRIE & COLLIGNON 1960). These beds are of marine, more precisely littoral, origin; but, besides *Triadobatrachus*, several other fossils are of continental origin (benthosuchid amphibians, plants). On the basis of the fish and amphibian fauna (LEHMAN et al. 1959), these marine levels are equated with the base of the middle part of the continental Sakamena group (outcroping in Southwestern Madagascar); therefore, these levels are equivalent to the local stage Gyronitian (BESAIRIE & COLLIGNON 1960). The Gyronitian corresponds to the Induan, that is early Triassic.

Abbreviations used in text-figures

ac:	acetabulum	h:	humerus	pt:	pterygoid
an:	atlantal neural arch	hv:	? articulatory head of 2nd vertebra	qu:	? quadrate
ar:	atlantal rib	i:	intermedium	r:	radius
atc:	bipartite atlantal centrum	il:	ilium	rb:	rib
c:	coracoid	is:	ischium	rd:	radiale
cl:	clavicle	las:	lamella alaris squamosi	rm:	ramus maxillari pterygoidei
co:	columella	lo:	lateral occipital	sc:	scapula
crb:	caudal rib	mtx:	matrix	ssc:	suprascapula
ct:	cleithrum	mx:	maxilla	scv:	6th caudal vertebra
c3:	centrale 3	n:	nasal	sph:	sphenethmoid
c4:	centrale 4	op:	opisthotic	sr:	sacral rib
d:	dentary	pa:	palatine	sv:	sacral vertebra
f:	femur	paf:	parietal foramen	t:	tibia
fb:	fibulare	pf:	? praefrontal	tb:	tibiale
fi:	fibula	ph:	parahyoid	th:	thyrohyal
fm:	fossa meckeli	pr:	prootic	u:	ulna
fop:	fontanella prootica	pra:	praearticular s.l.	ul:	ulnare
fp:	frontoparietal	psp:	parasphenoid	VI:	6th dorsal vertebra
				XII:	12th dorsal vertebra

Systematic Paleontology

Order Anura GIEBEL, 1845

Suborder: Proanura ROMER, 1945

Family: Triadobatradidae KUHN, 1962

According to ESTES & REIG (1973), the name of the family should not be Triadobatrachidae because the family name does not change when the name of the type genus is rejected as a junior synonym (International Code of zoological Nomenclature, 1964, art. 40); therefore, although *Triadobatrachus* KUHN, 1962 has replaced Protobatrachus PIVETEAU, 1936, the name of the family would be Protobatrachidae ROMER, 1945. Nevertheless, *Protobatrachus* PIVETEAU has not been rejected because of synonymy but because the name was preoccupied, that is it is a junior homonym. The name of a family is not valid if the name of its type genus is a junior homonym; the family name should be replaced by a name based on the valid name of the genus (Int. Code zool. Nomencl., 1985, art. 39). Therefore, Protobatrachidae, based on Protobatrachus PIVETEAU, is invalid and it should be replaced by Triadobatrachidae KUHN, 1962.

Genus: *Triadobatrachus* KUHN, 1962

Triadobatrachus massinoti (PIVETEAU, 1936)

1936a *Protobatrachus* nov. sp., PIVETEAU, p. 1607.
1936b *Protobatrachus Massinoti*, PIVETEAU, p. 1804.
1938   *Protobatrachus triassicus* n. sp., KUHN, p. 8.
1962   *Triadobatrachus* nov., KUHN, p. 328 — (*Protobatrachus* PIVETEAU 1937, non GISTL 1848; non *Probatrachus* PETERS 1878).

Redescription

In this description, "right", "left", "raised" and "depressed" apply to the cast structures, not to the holotype which is an external mold and in which the orientation is inverted. The fact that bone is never preserved and that observations have been made on casts (and checked on the holotype afterwards) has led to a problem: it is not always possible to determine whether an observed structure corresponds to bone or sedimentary figure; however, such a difficulty occurs in a very few cases.

The holotype (MNHN, n° MAE 126) is housed in the Institut de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.

Skull

(Text-fig. 2)

a) Exocranium. — One of the most conspicuous features of the skull roof is the frontoparietal. This bone displays low rugosities. According to PIVETEAU (1937: 145, fig. 6, 7) and WATSON (1940: 221) it is paired whereas HECHT (1962: 40) only admits that "there is, along the midline of the posterior half of the frontoparietal imprint, a faint line. ... It may ... represent ... a suture". The latter author misinterpreted WATSON's text, as he tells that (loc. cit.) "WATSON considered it a fused structure and indicates no such suture". However, WATSON (1940: 221) explicitely says that "... the brain case is covered by a pair of fronto-parietals ...". Similar misunderstanding can be found in the paper by ESTES & REIG (1973: 38) where it is stated: "HECHT (1962) notes that the frontoparietal may be paired, rather than single as PIVETEAU believed ...". However, PIVETEAU (1937: 144, 145) clearly writes "... un fronto-pariétal ... avec une trace de suture longitudinale ...", and refers to his figures 6 and 7, a median suture being clearly seen in the latter. Both the type-specimen and the casts demonstrate that a line (represented by a tiny ridge on the type-specimen) that is very probably a suture, runs from the posterior border of the frontoparietal to the level of an ovoid structure (see below) situated slightly left of the midline (the length of the frontoparietal in the midline is about 14 mm, that of the suture is approximately 7 or 8 mm). In the anterior half of the frontoparietal there is no conspicuous suture, but the table is markedly depressed along the median longitudinal axis. Therefore, it is possible to conclude that the frontoparietal was paired, or had been paired in earlier ontogenetic stages.
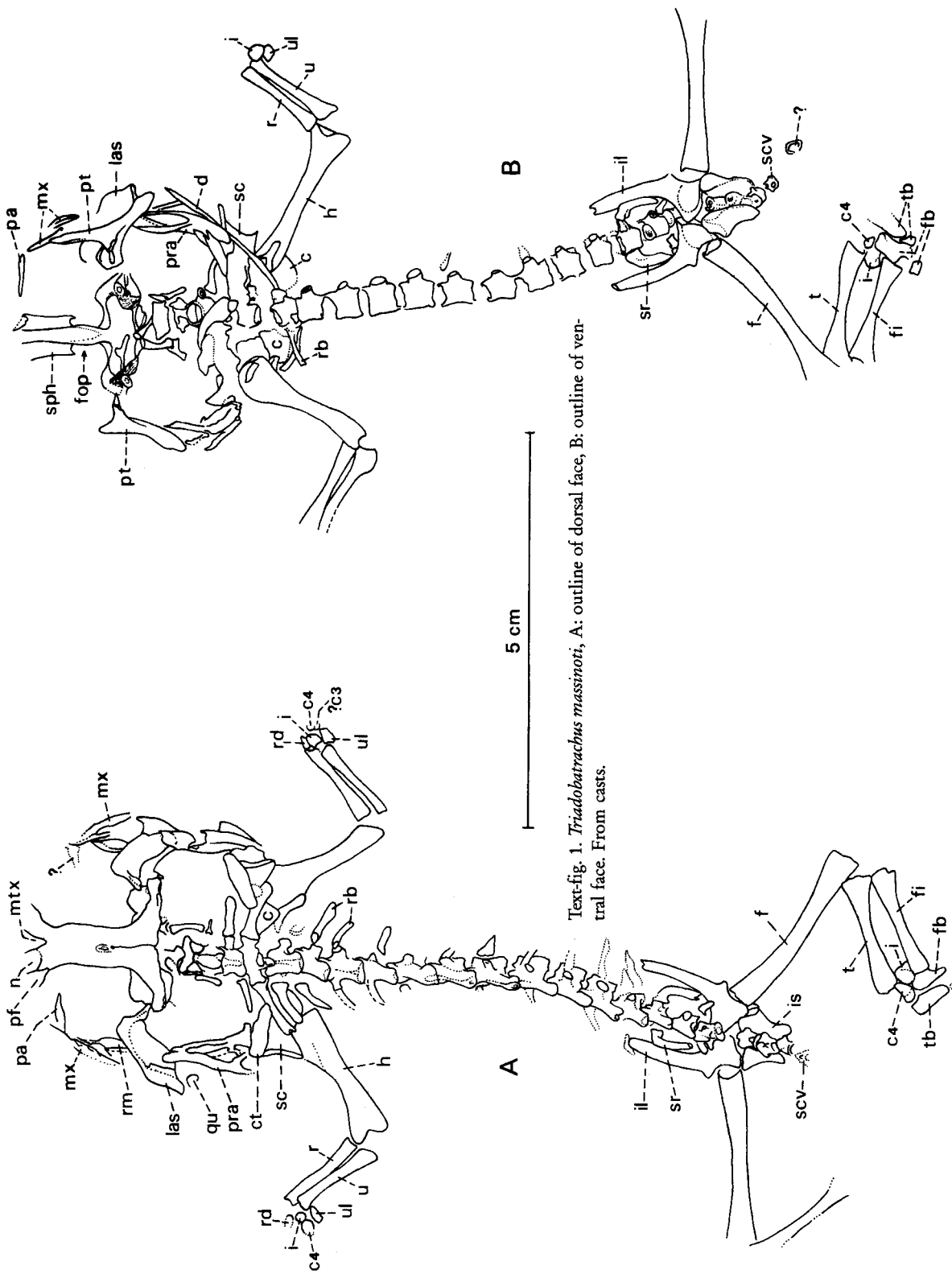
Text-fig. 1. *Triadobatrachus massinoti*, A: outline of dorsal face, B: outline of ventral face. From casts.

5 cm

About 6 mm from the posterior border of the frontoparietal, just behind the above mentioned ovoid structure, there is a distinct small depression in the midline, through which the median suture passes. This is probably the parietal foramen which escaped PIVETEAU's notice (1937: 145). HECHT (1962: 41) believes the parietal foramen may be "a clearly demarked ovoid area" which "lies not exactly in the median longitudinal axis but slightly to the right". Most probably he speaks about the aforementioned ovoid area that is located on the right of the midline on the type-specimen, that is to the left of the casts (see also GRIFFITHS 1963: 274). However, this structure is very slightly raised; therefore, it is probably a motif of the sculptured surface.

Laterally, the frontoparietals form ventral flanges whose ventral extension remains unknown but that is probably short. Posteriorly, the frontoparietals form strongly projecting lateral wings that partly cover otic capsulae; laterally, these wings slightly project beyond the capsulae and they were articulated with the squamosals (that are slightly displaced in the holotype). HECHT (1962: 42) suggested that the frontoparietal could include postparietals and tabulars; if the HECHT's opinion is right, the lateral wings would correspond to the tabulars. However, topographically, these wings might also correspond to supratemporals; but the possibility of a secondary extension of the frontoparietal cannot be ruled out.

A triangular markedly raised area anterior to the frontoparietals (corresponding to a depression on the type-specimen) was considered paired nasals by PIVETEAU (1937: 145, fig. 7), possible sphenethmoid by ESTES & REIG (1973: 38), and surface contact between the skeleton and matrix by HECHT (1962: 41). However, contrary to the PIVETEAU's drawing, there is no trace of median division of this area and hence nasals are excluded. Similarly is the sphenethmoid, because if it is exposed, it is never prominent above the level of the surrounding exocranial bones surface. Moreover, the surface of this area is very uneven and it does not correspond to a skeletal impression. Therefore, as was suggested in our preliminary report, a sedimentary structure should be concerned which is quite probable, this part of the fossil being located against one of the holes that open in the nodule and connect the internal mold to the outside (this hole corresponds to the intersection of the anterior part of the skull with the surface of the nodule).

A semicircular fragment of bone left of just mentioned sedimentary structure, together with another more lateral incomplete bone bordering the anteromedial section of the orbit are matter of another discussion. The lateral margin of the former fragment is slightly raised above the surface of the latter and of the frontoparietal which is perhaps slightly overlapped. Obviously this bone is a slightly disarticulated part of the dermal roof; it is most probably the nasal. This bone is not discernible on the right side.

The dermal bone that forms part of the orbital margin connects the frontoparietal very slightly below the dorsal surface of this latter bone. It should not be confused with the above mentioned semilunar element (presumed nasal), nor the latter should be considered its broken part, because limits of both bones are very clean and do not fit one another. The bone in question was considered the praefrontal by PIVETEAU (1937: 145, fig. 7) and SEDRA (1949: 639), the posterior extension of paired nasals, or the frontal processes of the maxillae by ESTES & REIG (1973: 38), or, possibly, the supraorbitotectal by JARVIK (1942: 549). If another terminology is used for the latter interpretation, the lacrimal might be concerned. It is difficult to decide which of these suggestions is correct. It only seems that the nasal is represented by the above semicircular element and does not reach posteriorwards the orbital margin. However, all other suggestions are equally possible and thus the identity of the bone fragment remains questionable.

Both squamosals lost their contact with the frontoparietals. When the original position of squamosals is reconstructed, the orbitotemporal vacuities display a wide anterior part posterolaterally prolonged by a narrower part. The anterior part of the dorsal surface of the lamella alaris squamosi is slightly sculptured; but there is a large semilunar smooth area, on the postero-dorsal surface, that served undoubtedly for the insertion of the cervical muscles (m. rhomboideus ant., m. sternocleidomasteoideus). The processus posterolateralis squamosi is either lacking or hidden in the space between the lamella alaris and the pterygoid (but see below).

Only posterior sections of both maxillae are preserved. Both seem to be approximately in their natural position, though disarticulated from the lamella alaris squamosi due to the slight displacement of both latter elements. On either side, the maxilla is represented by two elongate and separate parts; although the presence of an ectopterygoid should not be absolutely ruled out, it seems more probable that the inner part corresponds to the lamina horizontalis maxillae that was separated from the lateral wall of the bone (which was perpendicular to this lamina) by the crushing of the fossil. No teeth are apparent.

The parasphenoid is, except for its anteriormost tip, well preserved, and maintains ist original position in relation to the endocranial structures. It shows the T-shape morphology that occurs in nearly all anurans. Postero-lateral
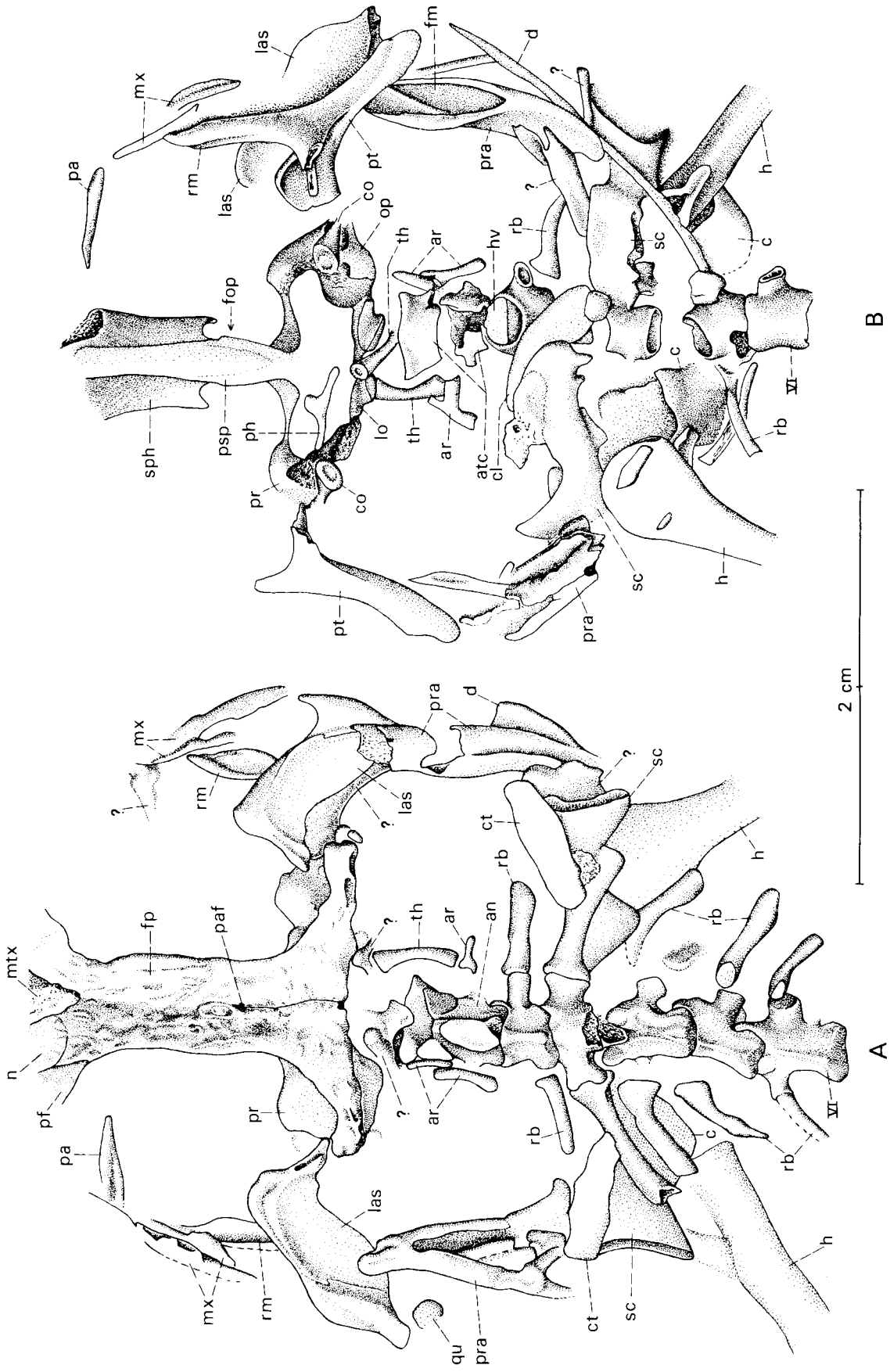
Text-fig. 2. *Triadobatrachus massinoti*, A: anterior part of dorsal face, B: anterior part of ventral face. From casts.

2 cm

corners display curved emarginations that bordered the fenestra ovalis; thus, the latter fenestra faced more or less ventrally. This condition is somewhat reminiscent of the middle/late Jurassic *Notobatrachus* (ESTES & REIG 1973: 20 and fig. 1—5). The pterygoid is triradiate, as in anurans. The tips of rami maxillares are seen in the dorsal cast as pointed elements coming from below the lamellae alares squamosi. In dorsal view, both rami maxillares of the pterygoids display grooves that housed cartilaginous parts of the palatoquadrate. Deep and thin lamellae extend ventrally from the rami interiores of the pterygoids; their extent and connections remain unknown. From these rami interiores arise strong dorsal processes, the left one is well exposed on the ventral cast; it may be wonder whether this process is the processus posterolateralis squamosi that would join the pterygoid and would be fused to it. Both pterygoids being slightly displaced, contacts with the otic capsules and the maxillae are lost in the specimen.

The palatine is exposed within the left orbit. This caused much confusion, as PIVETEAU (1937: 147) stated that it is located slightly above (above on the figure, in fact anterior on the specimen) the articulation between the maxilla and the anterior ramus (= ramus maxillaris) of the pterygoid and accordingly draw it on his restoration of the skull in ventral aspect (PIVETEAU, l. cit., fig. 3), but not on his fig. 7 (reconstruction of the skull in dorsal aspect), though the element within the left orbit is well seen also dorsally. This reconstruction based on incorrect relations to the pterygoid (and maxilla) was endorsed with some modifications by WATSON (1940, fig. 18) and ESTES & REIG (1973, fig. 1—13). In all these reconstructions the palatine would have been a thorn protruding into the orbit. However, such a disposition would be non-functional and inconceivable. The palatine, in such a reduced size, always maintains its topographic relations to the postnasal wall and adjoins it ventrally, fusing in anurans either with the maxilla or with the vomer (Roček 1981, fig. 59). Obviously, the postnasal wall is situated more anteriorly than is the preserved position of the palatine. Besides, although maxillae seem to be approximately in their original position and both orbits are exposed in about the same extent, the right palatine is not seen (on the right side of the dorsal view, a faint trace which is perhaps a bone appears approximately symmetrical to the left palatine; because of its shape, this trace cannot correspond to the right palatine). It seems that there is a thin strip of sediment between the left palatine and the maxilla. Thus it is possible to conclude that the palatine was displaced posteriorwards from the ventral surface of the postnasal wall, that is its original position, and that although it was already reduced to the extent found in anurans, it was not yet firmly fused to the maxilla.

The position of the lower jaw was discussed in detail (see HECHT 1962: 40; GRIFFITHS 1963: 274; ESTES & REIG 1973: 38). The latter authors expressed some doubts as for its interpretation, but it is necessary to take into consideration that the quadrate/jaw joint is not preserved (see Text-fig. 2) and that the whole jaw is not only reflected back against the ventral face of the thorax but also rather shifted anteriorwards onto the dorsal surface of the lamella alaris squamosi. Each half of the jaw consists of two parts, as noted by GRIFFITHS (1963: 274), the praearticular s. l. and the dentary. There is no evidence of teeth. The groove on the praearticular housed MECKEL's cartilage, as suggested by HECHT (1962: 40); it is open ventrolaterally and in original state it was covered by the dentary. A fossa Meckeli is preserved on the praearticular s. l. An attempt to reconstruct jaw musculature was made by CARROLL & HOLMES (1980: 31—32).

A small and well defined bone widely bifurcated posteriorly, preserved on the posterior part of the parasphenoid, was interpreted as parahyoid bone by PIVETEAU (1937: 148). Two small elongated and rather curved bones are preserved in the cervical region. One is located immediately posterior to the right occipital condyle, the second lies between the foramen magnum and the atlas, between both condyles. They were interpreted by PIVETEAU (1937: 148) as thyrohyals. It seems that nothing contradicts these interpretations. Between the skull and the atlas, an indeterminate structure appears in dorsal view.

On the posterolateral tip of the right squamosal there is a squarrish element that was considered by PIVETEAU (1937, fig. 7) the quadrate. However, the casts clearly demonstrate that this is a fragment of the posterior part of the mandible (praearticular s. l.). If carefully investigated, the continuity of this element with the main part of the bone may be traced along its medial surface.

No element that could be determined as the quadratojugal is discernible. The reasons why PIVETEAU (1937, figs. 3 and 7) had no doubt about the presence of this bone are probably based on the presence of a distinct line that runs approximately between the smooth and sculptured surfaces on the lamella alaris squamosi, and on the statement (PIVETEAU 1937: 146) that "… une troisième branche (of the squamosal; authors' note) … qui descend jusqu'au carré et s'articule avec le quadratojugal … ces connexions … sont constantes chez tous les Tétrapodes primitifs".

b) E n d o c r a n i u m . — The sphenethmoid is preserved only in its posterior section that formed part of the braincase. While the ethmoidal region including postnasal walls is lacking (out of the nodule that contains the fossil), its posterior margin is well preserved. It is apparent that between the sphenethmoid and prootics, the braincase walls consisted of cartilage and soft tissue. All the pertinent cranial nerves (III—V) passed from the braincase through the foramina and fontanelles of this part of the braincase.

The otic capsules consist of three elements (the prooticum, the opisthoticum, and the occipitale laterale). As is well seen on the ventral cast, the opisthotic and lateral occipital were probably separated by a slender strip of cartilage, as is the case in juvenile specimens of some Recent anurans. The drawing by PIVETEAU (1937, fig. 3) is inaccurate; the opisthotic extends farther medially (and therefore is larger) than in the PIVETEAU's reconstruction. According to ESTES & REIG (1973: 39), the bone rightly identified as an opisthotic by PIVETEAU (1937: 142, fig. 3) could actually be an operculum. This bone is in fact a part of the posterior wall of the otic capsule, therefore it cannot be an operculum. The left opisthotic is displaced and the right one is partly broken off.

The columellae are well seen on both sides. They do not retain their original position, their distal tip being displaced dorsally. The proximal section of each columella is far more stout than the distal one, and was probably completed by a cartilaginous ring. The medial face of the columella displays a depression which is reminiscent of the *Doleserpeton* stapes illustrated by BOLT & LOMBARD (1985). Unfortunately, on both sides of the fossil, this medial face is not enough clearly exposed and the presence, or absence, of the posterior notch known in living anurans and "advanced" temnospodyls (BOLT & LOMBARD 1985: 87) cannot be checked with certainty (however, it is apparently lacking). The columella is rather flattened, which follows from the comparison between the columellae of the right and left sides.

A small ovoid bone behind the posterolateral part of the left squamosal (seen in the dorsal cast) might be the quadrate.

Postcranial skeleton

a) V e r t e b r a l c o l u m n (Text-figs. 1, 2, 3, 4). — The centrum of the atlas is composed of anterior and posterior separate parts, but its neural arc is single. Two cervical cotyles are attached to the anterior face of the centrum; they are clearly, although not widely, separate. On both sides, on the anterolateral surface of the neural arch, there are small distinct areas that took part in the craniovertebral articulation. ESTES & REIG (1973: 39) correctly identified a bifurcated element to the right of the atlas, clearly visible on the ventral cast, as a bicapitate rib belonging to the atlas. However, both its proximal heads as well as its distal section are broken off. Left atlantal rib lies parallel to the vertebral column axis left to the atlas; it is rather turned along its longitudinal axis, so that one of the two proximal rami was directed ventrally and is broken near its base. The nature of the articulation of both atlantal ribs to the vertebra may be reconstructed from the projections on the left surface of the bipartite centrum well seen on the ventral cast. One articulation process is born on each part of the centrum; both processes lie in a plane that is almost horizontal. It may be supposed that both parts of the centrum were connected by cartilage in the living animal, so that their original distance is retained. The distance between the articulation processes corresponds approximately to that between the reconstructed heads of the pertinent ribs.

The second vertebra, if observed in the ventral cast, displays a distinct semilunar element which is convex anteriorly. It could be considered as remains of an intervertebral disc or slightly displaced articulation head. If the latter interpretation is correct, this vertebra would be opisthocoelous (as the only one within the whole column). The right rib of this vertebra is still articulated with its processus transversus, the left one is slightly disarticulated. Both ribs (similarly to all others belonging to more posterior vertebrae) are single-headed.

The third vertebra is not very long but its transverse processes are very massive; the ribs are the longest and strongest. The view introduced by PIVETEAU (1937: 161, fig. 21; see also KUHN 1962, fig. 1 and ESTES & REIG 1973, fig. 1—13) that these ribs are bifurcated laterally is not correct. In fact they are straight and, on each side, the dorsal end of the cleithra abuts against them (Text-figs. 1 A, 2 A).

The neural arch of the 4th vertebra is long. The posterior part of the 3rd vertebra neural arch being broken off, the prezygapophyses of the 4th vertebra are exposed; their articular surface is oval and plane. A low sagittal keel occupies the posterior two thirds of the neural arch length. On the right side, a short and stout transverse process is exposed; the rib that was articulated with it is slightly displaced laterally. The vertebra being tilted, the opposite
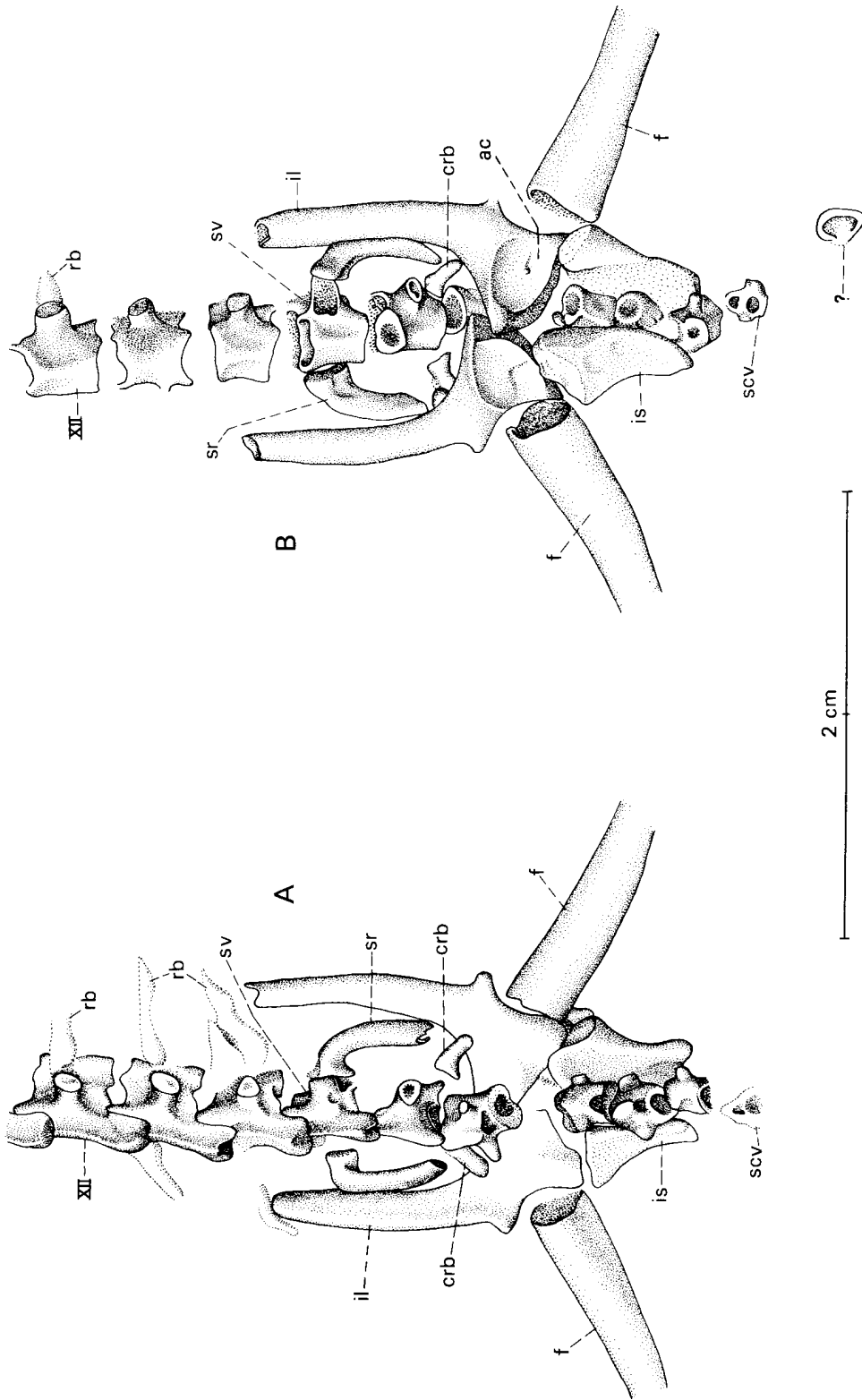
Text-fig. 3. *Triadobatrachus massinoti*, sacral and caudal regions. A: dorsal face, B: ventral face. From casts.

2 cm

transverse process is not observable. The centrum of the vertebra is markedly shorter than the neural arch (about half the length of the latter). It is cylindrical and clearly amphicoelous.

Up to the 14th vertebra, the vertebral morphology is similar to that of the 4th vertebra; these vertebrae bear ribs that were short but whose length cannot be precisely evaluated. The right lateral wall of some of these vertebrae is exposed; apparently, foramina for spinal nerves are lacking.

The 15th vertebra is the sacral one. It is rather short but strong and its neural arch seems narrow; it is provided with stout transverse processes that articulate with strong and caudally recurved sacral ribs.

Six caudal vertebrae are exposed. The section of the neural canal of the last visible vertebra remains well shaped, therefore this vertebra was not the last one and the length of the tail was probably longer than supposed. This was already suggested by HECHT (1962: 40). Only one pair of caudal ribs is apparent but it is not possible to establish whether it articulated with the first or the second caudal vertebra. These two ribs are short, stout and practically straight. It may be wonder whether their lateral tip contacts either the sacral rib or the ilia, and thus supports the pelvic girdle (Text-fig. 4). It seems that at least all visible caudal vertebrae could have borne ribs as they possess marked transverse processes. On the ventral face of the cast, posteriorly to the last caudal vertebra, the section of an un-determined bone is exposed.

In sum, there are 14 praesacral (including one atlas), 1 sacral and 6 exposed caudal vertebrae within the vertebral column. All (except perhaps the second) are amphicoelous, and probably all bear free ribs.

b) Pectoral girdle (Text-figs. 1, 2, 4). — This structure is rather badly crushed. Its constituent parts are dis-placed and intermingled with ribs and fragments of the lower jaw.

A curved, flat and elongate bone located obliquely across the ventral surface of the second vertebra is probably the clavicle that apparently turned along its axis because its convexity is anteriorly oriented. The curved shape of the clavicle indicates that the girdle was not firmisternal; it could have been arciferous or of another type unknown in Recent anurans. Neighbouring large elements may be interpreted as scapulae (scapulocoracoids according to PIVE-TEAU 1937, fig. 23). The right scapula is clearly exposed on the ventral face of the fossil, its dorsal part emerges on the dorsal face, between the distal section of the third rib and the cleithrum. Similar situation is observable on the left side.

On the ventral face, massive, flat and arched bones appear on either side of the vertebral column. They might be fragments or exposed parts of the coracoids (the right one is the "plaque coracoïdienne" of PIVETEAU, op. cit., fig. 23). On the right side, in ventral view, a flat element lies below the coracoid; it might correspond to a crushed part of the coracoid (in such a case, the coracoid would have been very large) and dorsally it appears below the right rib of the third vertebra. On the left side, a symmetrical arched element appears in dorsal view below the ribs of the third and fourth vertebrae and it lies dorsal to the scapula. This interpretation according to which the scapula and coracoid are separate rather differs from our previous one (RAGE & ROČEK 1986: 257) in which the former element (i. e. the scapula) was considered as a scapulocoracoid; we are led to this new interpretation because there is no other explanation for such comparatively robust elements located close to the proximal heads of both humeri than that they are the coracoids or parts of these bones. Despite this new interpretation, on either side, a large and flat element remains unidentified, unless it is a part of the coracoid (see above). Anyhow, the pectoral girdle comprised large bone surfaces. No other ventral element of the pectoral girdle than the clavicle and coracoid is known.

Both cleithra are well seen on the dorsal cast, pressed against the dorsal face of the ribs of the 3rd vertebra. Originally they were considered branches of bifurcate ribs (see above). There is no trace of the suprascapula; it was apparently cartilaginous as in modern anurans. Those elements that were designated as the suprascapula and cleithrum by PIVETEAU (1937, fig. 23) are in fact parts of lower jaws.

c) Pelvic girdle (Text-figs. 1, 3, 4, 5). — Its components are slightly disarticulated. The ilia are elongated and in the living animal were completed by cartilaginous anterior tips as demonstrated by their hollowed-out extremities. The preserved length of the ilial shaft corresponds to about that of the last three praesacral vertebrae. On the medial face of the acetabular part there is not any trace of an interiliac tubercle. Such tubercles are encountered in forms that are aquatic and generally considered primitive: Pipidae, Palaeobatrachidae, Discoglossidae (HECHT & HOFF-STETTER 1962; VERGNAUD-GRAZZINI & HOFFSTETTER 1972; ESTES & SANCHIZ 1982). There is a distinct tuber on the dorsal border of either bone. The ilium/sacral rib articulation is unusual; the sacral rib being recurved, most of its length

was in contact with the medial face of the ilium shaft. The ischia stretch posteriorly and were connected with ilia either syndesmotically or synchondrotically. Both pubes are lacking; it is supposed that they were cartilaginous, as in modern anurans. The large acetabula are exposed on the ventral surface of the holotype.
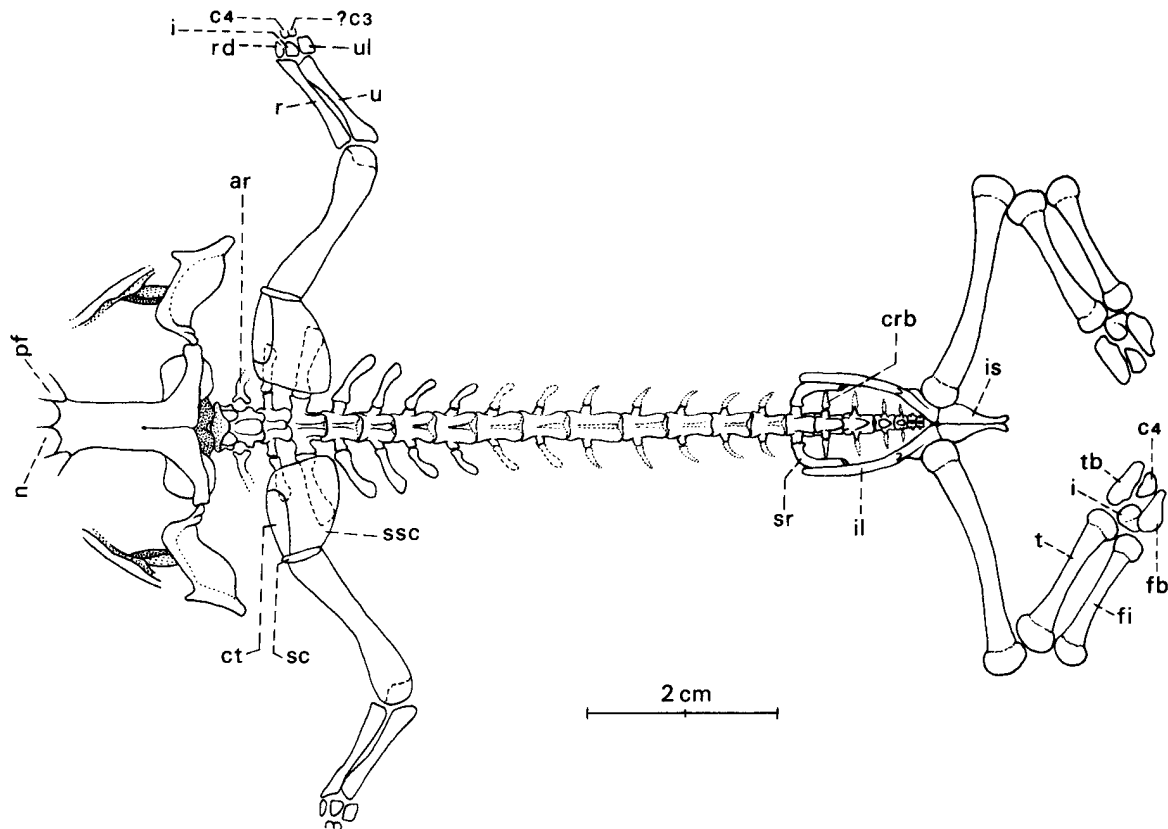
Text-fig. 4. *Triadobatrachus massinoti*. Restoration of known parts, dorsal view; suprascapula and relations between sacral ribs and first caudal ribs hypothesized (Nota: tail incomplete in order that the dorsal part of the ischia remains exposed; all known caudal vertebrae may have borne ribs).

d) **F o r e   e x t r e m i t y** (Text-figs. 1, 4). — The proximal part of the humerus forms a well developed ventral crest. Its distal end is wide; obviously the epiphysis was unossified and hence lacking in fossil. Two epicondyles are more or less distinct. The radius and ulna are separate and markedly shorter than the humerus (about two thirds of the humerus length). The right limb displays the proximal row of carpal elements which comprises three ossicles that may be regarded as the radiale, intermedium, and ulnare, plus the centrale 4 (centrale 1 in another terminology) and perhaps centrale 3 (centrale 4 in another terminology).

e) **H i n d   e x t r e m i t y** (Text-figs. 1, 4). — The femora are long, cylindrical and narrowed in their median part. They are not straight but very slightly sigmoid, suggesting thus morphology of the femur in modern anurans. The proximal epiphyses are lacking, as they were probably cartilaginous (the distal ones are unknown, being located out of the nodule). The tibia and fibula are separate and markedly shorter than the femora. Four tarsal elements of the right hind limb are known. Two of them are elongate but less so and more massive than in the restoration by Pive-teau (1937, fig. 29), Estes & Reig (1973, fig. 1—13) and Jarošová (1974, fig. 6). These two bones are the tibiale and fibulare. The other two bones are small; they have been regarded as sesamoid bones by Piveteau (loc. cit.: 166). Hecht (1962: 42) demonstrated that this identification is wrong. Estes & Reig (1973: 39) and Jarošová (1974: 132) came to the conclusion that these two bones are the intermedium (the proximal element) and the centrale 4 (centrale 1 by Jarošová who used a different terminology). This identification is probably correct.

Relations of *Triadobatrachus* with anurans

Most of the previous authors (except e.g. HECHT 1960: 356) agree that similarities between *Triadobatrachus* and anurans reflect their true phylogenetic relationships. It also seems to be clear now that the specimen does not represent a larva as was suggested by GRIFFITHS (1956: 342—343; 1963: 275—276) but that it corresponds to an adult: dermal skull bones are fully developed, the columella is of definitive size, presumed parahyoid and thyrohyals are ossified (for detailed discussion see RAGE & ROČEK 1986: 257).

In order to demonstrate that *Triadobatrachus* is a larva, GRIFFITHS (1963: 275—276) put forward several features: ilia only moderately elongate, lack of functional sacrum (that is transverse processes not fused to sacral ribs), tail built by articulated vertebrae, tibia and fibula on one hand and radius and ulna on the other hand not fused, femur to tibio-fibula ratio of relatively high value. These characteristics may be considered as larval features only if it is supposed a priori that *Triadobatrachus* being an anuran, its skeleton should display characteristics of modern anurans. But these characteristics are only primitive ones, also known in adults of various labyrinthodonts, that were still retained by primitive members of the line of evolution that has led to modern anurans. The so-called "parietal recess" of GRIFFITHS, another supposed larval characteristic of *Triadobatrachus*, turned to be a motif of the sculptured surface (see p. 6) and not a groove traversed by a fibro-nervous tract connecting the habenular region of the brain with a larval "Stirnorgan" (cf. GRIFFITHS 1963: 276). Neither separation of the upper and lower jaw elements could serve as a good basis to consider *Triadobatrachus* a larva. It was concluded in our preliminary paper (RAGE & ROČEK 1986: 257) that *Triadobatrachus* represents a post-metamorphosed but not yet fully matured animal, which is evidenced by the lack of the epiphyses of the long bones.

Taken as a whole, several advanced features of *Triadobatrachus* are characteristic of anurans: frontal and parietal fused, wide orbits merging with postero-lateral vacuities, parasphenoid T-shaped, pterygoids deeply triradiate, palatal structures reduced, palatine bone lying transversally, ilium anteriorly projecting, pubis cartilaginous. To these characters it may be added that the hyoid was possibly anuranlike and that the possible absence of teeth is also reminiscent of anurans. Therefore, *Triadobatrachus* is considered closely related to anurans and it may be even regarded a member of this group.

The determination of precise relationships between anurans and *Triadobatrachus* deserves attention. The simple statement that *Triadobatrachus* is an ancestor of anurans, more advanced in its cranial skeleton than in the postcranial one, seems to be insufficient on the background of the character diversity found in anurans. The first problem is caused by the composition of the frontoparietal. In some anuran lineages (e.g. Pelobatidae sensu ROČEK 1981) there is, besides frontal and parietal ossification centers, also an unpaired median element adjoining the tectum synoticum. In adults, these five elements fuse altogether. However, in some forms, the mentioned odd element retains its independency also in postmetamorphosed individuals (e.g. recently found fossil from Green River formation, still to be described by ESTES & GRANDE). If the odd element is incorporated into the frontoparietal complex, the median suture can never reach its posterior margin.

In *Triadobatrachus*, regardless of the rather obscure nature of the frontoparietal in its anterior part, the posterior portion is clearly divided by a median suture. Thus, there is no median element contributing to the building of this complex in its posterior part.

The question now arises what is the nature of the odd element. Two explanations may be proposed. First, it is an evolutionary neomorph that had arisen within the posterior section of the interparietal median suture during the period of evolution from *Triadobatrachus* to those anurans which have this element. It is known that additional ossifications occasionally can be found within the anterior section of the interfrontal suture in some anurans, which are commonly termed "interfrontals", "internasofrontals" or "postrostrals" (CHUGUNOVA 1981: 117, 120, figs. 1, 2, 3) (these should be distinguished from "co-ossified ethmoid" or "dorsal sphenethmoid", as both these terms concern in fact an uncovered dorsal surface of the sphenethmoid). However, as these bones considerably vary both in shape and location, they may be considered only islets of ossifying tissue, not true ossification centers.

The second explanation may be that the mentioned element is the heritage from the ancestors. However, the problem of homology (either with median extrascapular of crossopterygians or with some other elements) is complicated by the fact that in the process of evolution from crossopterygians to anurans (via some, not-yet-known labyrinthodonts) the otic region of the skull was considerably shortened. This, together with the fact that already in ichthyostegids (e.g. *Acanthostega*) there is a paired instead of unpaired element [it is worth of note that according to

JARVIK (1980: 241, fig. 171), in *Ichthyostega* it also lost its former identity by incorporation in the parietals] and that, as far as it is known, among labyrinthodonts only one specimen of *Aphaneramma* (Trematosauridae) has a similar unpaired element, suggests that fused postparietals might be concerned in these non-anuran forms. If this hypothesis is accepted, then postparietals not only have not fused with each other but even disappeared in *Triadobatrachus* (HECHT 1962: 42, however maintains that they can be included into the frontoparietal in *Triadobatrachus*), while in some other anuran lineages they could fuse together and also with neighbouring parietals. Similar situation is found in most reptiles and in some mammals (in rodents and ruminants the so-called "interparietal" is embryologically of paired origin, and only later it fuses both with each other and with parietals).

A peculiar feature of the frontoparietal in *Triadobatrachus* is its lateral extent in its posteriormost part. It reaches the level of the crista parotica, wich is a unique condition, not only if compared with anurans, but also if comparison is made with labyrinthodonts.

Another problem which makes estimation of affinities of *Triadobatrachus* and anurans difficult is the structure of the pectoral girdle. In anurans two types of the girdle occur, commonly termed arciferous and firmisternal. Until now, there is no evidence of that one could evolve from the other. If the condition in *Triadobatrachus* corresponds to the arciferous type as it is possible, it would be hard to explain the origin of the firmisternal one. Other difference in which one character state cannot be derived from the other can be found also in ontogeny of various anurans. As an example can serve different types of innervation of the tail musculature (WASSERSUG, in verb.) and different patterns of development of the ethmoidal region (ROČEK, in press).

We are thus in paradoxal situation that relationship between *Triadobatrachus* and anurans cannot be fully understood at present state of knowledge not because of insufficient knowledge of the former, but because of not yet satisfactory explained diversity within anurans. For this reason we consider detailed conclusions in this respect as premature.

## Remarks on saltatorial adaptations in anurans

HECHT (1962: 42) pointed out the anuran-like structure of the skull in *Triadobatrachus*, contrasting with rather primitive features of its postcranial skeleton. The anuran skull structure would be the result of the strengthening of the sagittal axis, i.e. development of fused frontoparietal, in order to compensate for the enlargement of the orbito-temporal vacuities. It was concluded in our previous paper (RAGE & ROČEK 1986: 258) that judging by *Triadobatrachus*, first evolutionary changes towards anurans occurred in the skull and saltatorial locomotion only followed later. Although saltatorial adaptation was incipient in *Triadobatrachus* (trends towards elongation of ilia and elongation of tarsal elements), it was probably not a specialized jumper.

Thus the question arises what was the reason for elongation of the ilia and why the pubis lost its ability to ossify. Main muscles inserting onto the elongated portion of the ilia (ala ossis ilii) in anurans (see e.g. GAUPP 1896: fig. 106) are M. obliquus externus, M. transversus (both taking part in the formation of the flanks of the trunk). M. iliacus externus (running to the trochanter femoris, i.e. to the proximal part of the hind extremity), M. tensor fasciae latae (not very important for locomotion), M. iliacus internus (abductor of the femur) and M. coccygeo-iliacus (connecting the ilium to the urostyle). Therefore, several of these muscles belong to the trunk and only the iliacus internus muscle plays a significant role in locomotion. It should be noted that this muscle originates close to the acetabulum, within the complex of other muscles responsible for locomotion, not on the anterior elongate part of the ilium. All other locomotor muscles of the posterior extremity surround the acetabulum. One may deduce that prolongation of the ala ossis ilii was caused by other reasons than by the need for a muscle insertions area.

As the anteriormost muscles of the ala belong to the trunk and the acetabulum is located laterally to the urostyle (that is the former caudal part of the rachis), the acetabular level, in other words the level of the hind limb proximal joint, was shifted posteriorwards with respect to the sacrum. This posteriorwards shift of the acetabular level was accompanied by the simultaneous strong shortening of the praesacral part of the vertebral column, that is anteriorwards shift of the sacrum. The shift of the acetabular region posteriorwards is seemingly in contradiction with the reduction of the number of praesacral vertebrae. This paradox is explainable by the need for the rigidity of the body axis (GANS & PARSONS 1966: 96). In *Triadobatrachus* the ilia are only moderately elongated (i.e. the acetabulum moved only slightly posteriorly), the number of praesacral vertebrae is still comparatively high, and anterior and posterior limbs display

similar lengths. This anatomical condition could have allowed quick crawling (like in *Bufo calamita* for example) but certainly not effective jumping.

More difficult to explain is the cartilaginous pubis. This state was probably already present in *Triadobatrachus*. In anurans it serves for the insertion of several muscles important in saltatorial locomotion. However, it is important to note that none of them is inserted exclusively on the pubis; every insertion continues onto adjacent ilia or ischia. Neither it is possible to suggest that cartilaginous pubis would offer some kind of elasticity that would help to absorb bumps in jumping because this was probably not yet useful in *Triadobatrachus*.
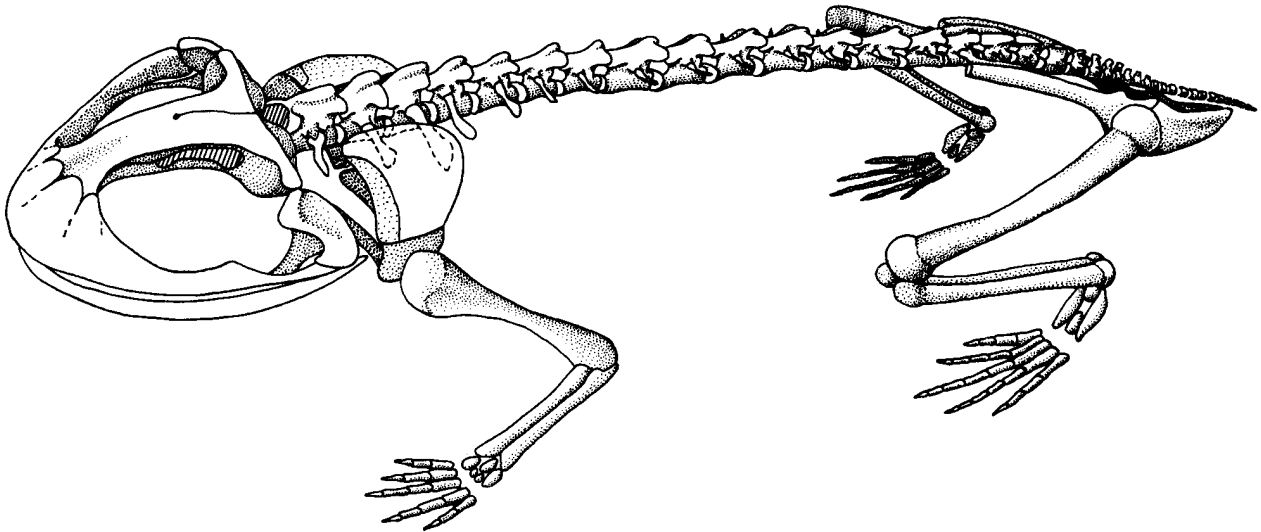
Text-fig. 5. *Triadobatrachus massinoti*, hypothesized restoration. Total length about 10 cm.

At last, it may be concluded that *Triadobatrachus* was not a true and efficient jumper (RAGE & ROČEK 1986). From this remark arises a problem: as a whole, Anura appear as an assemblage more or less highly adapted to saltatorial habits whereas the oldest known member of the group (*Triadobatrachus*) does not display limb adaptations to such a mode of life. Therefore, it may be wonder what was the impetus that caused the origin of anurans; saltatorial habits could have been only secondary adaptations. This is perhaps connected with the observation by SANCHIZ (1986) who noted that the locomotor apparatus of *Triadobatrachus* is markedly different from that of the theoretical ancestor of the group reconstructed on the basis of modern forms.

Conclusions

One can conclude that *Triadobatrachus* clearly displays evolutionary trends toward anurans. Some characters (e. g. orbit size, fusion of frontoparietals, morphology of pterygoids and squamosals, etc.) are developed to the same degree as in modern anurans, but other features, mainly in postcranial skeleton, still maintain rather primitive nature. Relationships of *Triadobatrachus* with anurans are indisputable although not precisely known, but on the other hand its relations with Palaeozoic amphibians are still unknown.

Summary

1. New investigations reveal that the palatine which is exposed within the left orbit was most probably displaced posteriorwards from its original position on the ventral surface of the postnasal wall, and although it was already reduced to the extent found in modern anurans, it was still free. It might be also supposed that the tail was longer than displayed on the specimen, because of the well developed neural canal in the

very posterior exposed caudal vertebra. Both cleithra lean dorsally on the ribs of the 3rd vertebra; they were hitherto considered branches of bifurcate ribs.

2. Most of the characters believed to favour the view that *Triadobatrachus* is a larva are refuted.

3. The anatomical structure of *Triadobatrachus* suggests that the evolution towards anurans started with modifications on the skull, not with changes in locomotory system.

4. Differences in the structure of *Triadobatrachus* and some anuran lineages, as well as diversity in some characters present in anurans does not allow yet any precise conclusions as for their relationships, except for the general statement that *Triadobatrachus* is close to anuran ancestor.

5. Saltatorial locomotion did not cause only elongation of the ilia, but also posteriorwards shift of the acetabular portion. This is evidenced by trunk muscles that occupy most part of the ala ossis ilii; locomotory muscles are concentrated around the acetabulum. Besides compensation of the vertebral column shortening, the reasons of ilia elongation was most probably the need for the body rigidity, similarly to birds.

6. The pubis remained cartilaginous already in *Triadobatrachus*. As it plays a significant role in the insertion of locomotory muscles, the reason why ossification does not occur remains obscure. Biomechanical reasons are excluded, because *Triadobatrachus* was not yet capable of true and effective jumping.

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