The scapulocoracoid of an Early Triassic stem-frog from Poland

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The scapulocoracoid of *Czatkobatrachus polonicus* Evans and Borsuk-Białynicka, 1998, a stem-frog from the Early Triassic karst locality of Czatkowice (Southern Poland), is described. The overall type of scapulocoracoid is plesiomorphic, but the subcircular shape and laterally oriented glenoid is considered synapomorphic of Salientia. The supraglenoid foramen is considered homologous to the scapular cleft of the Anura. In *Czatkobatrachus*, the supraglenoid foramen occupies an intermediate position between that of the early tetrapod foramen and the scapular cleft of Anura. The cleft scapula is probably synapomorphic for the Anura. In early salientian phylogeny, the shift in position of the supraglenoid foramen may have been associated with an anterior rotation of the forelimb. This change in position of the forelimb may reflect an evolutionary shift from a mainly locomotory function to static functions (support, balance, eventually shock-absorption). Laterally extended limbs may have been more effective than posterolateral ones in absorbing landing stresses, until the specialised shock-absorption pectoral mechanism of crown-group Anura had developed. The glenoid shape and position, and the slender scapular blade, of *Czatkobatrachus*, in combination with the well-ossified joint surfaces on the humerus and ulna, all support a primarily terrestrial rather than aquatic mode of life. The new Polish material also permits clarification of the pectoral anatomy of the contemporaneous Madagascan genus *Triadobatrachus*.

Key words: Anura, Salientia, *Triadobatrachus*, *Czatkobatrachus*, pectoral girdle, Triassic, Poland.

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Introduction

Czatkobatrachus polonicus Evans and Borsuk-Białynicka, 1998 is a stem salientian described from the Lower Triassic microvertebrate locality of Czatkowice in southern Poland (Paszkowski and Wieczorek 1982). It is the earliest representative of this lissamphibian group known from the Triassic of northern Pangea, and only the second recovered from Triassic deposits, the roughly contemporaneous *Triadobatrachus massinoti* (Piveteau 1936) from Madagascar being the first.

Czatkobatrachus and *Triadobatrachus* are the only taxa spanning the enormous gap in early salientian evolution between possible dissorophoid ancestors (e.g., Bolt 1969; Milner 1988; Shishkin 1973) of Permian age and the earliest frogs from the Lower and Middle Jurassic: *Prosalirus* (Shubin and Jenkins 1995), *Vieraella* and *Notobatrachus* (Baez and Basso 1996), *Eodiscoglossus* (Evans et al. 1990).

To date, only a few postcranial bones of *Czatkobatrachus* (ilia, distal humeri, ulnae and vertebrae) have been described

(Evans and Borsuk-Białynicka 1998) from amongst the disarticulated material from Czatkowice (Borsuk-Białynicka et al. 1999). Incomplete as they are, the remains of *Czatkobatrachus* are similar to those of *Triadobatrachus* but appear more derived in rib and vertebral structure and in the degree of ossification of the elbow joint.

The objective of the present paper is to describe newly discovered material of the scapulocoracoid of *Czatkobatrachus polonicus* and to discuss the polarity of character states in this part of the postcranial skeleton. We do not aim to construct a new cladogram of Salientia based on a single element, but rather to fit the observed characters to existing cladograms (Evans and Borsuk-Białynicka 1998; Milner 1988, 1993; Ford and Cannatella 1993; Sanchiz 1998). This permits a reconstruction of the possible sequence of character state evolution through the phylogeny of the salientian clade, and sheds some light on the development of frog locomotion.

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The structure of the scapulocoracoid of *Czatkobatrachus* permits a better understanding of pectoral girdle structure in *Triadobatrachus*.

The material comes from Lower Triassic bone breccia deposited in a single fissure (Czatkowice 1) developed in the Lower Carboniferous limestone quarry of Czatkowice (Cracow Upland, Poland). The karst infillings were discovered in 1978 by a team from the Institute of Geological Sciences of Jagiellonian University, Cracow, under the supervision of Dr. J. Wieczorek, and were then explored by the same team (Paszkowski and Wieczorek 1982). In 1979 all the material was generously transmitted to the Institute of Paleobiology and Museum of the Earth, both Polish Academy of Sciences, Warsaw, for palaeontological investigations. The samples consist of a fine-grained sandy yellow limestone, with some calcite cement, and include bones. They were subjected to a time-consuming process of chemical preparation, using acetic acid to break down the matrix. This preparation is still in progress. The resulting material consists of thousands of damaged and disarticulated bones, and is housed mainly in the Institute of Paleobiology, and partly in the Museum of the Earth (Borsuk-Białynicka et al. 1999). With about 50 specimens of disarticulated bones, *Czatkobatrachus polonicus* (Evans and Borsuk-Białynicka, 1998) constitutes only a very small percentage of the whole collection. Most specimens belong to small archosauromorphs, lepidosauromorphs, and procolophonids, while small temnospondyls and fishes are very rare (Borsuk-Białynicka et al. 1999). The microvertebrate assemblage remains under study.

The karstification phase at Czatkowice 1 may have lasted from the Late Permian to the Early Triassic, no later than the Scythian (about 238 Ma) when the whole region was submerged by the Roth Transgression. The composition of the assemblage suggests a late Olenekian age, but present evidence is not unequivocal (Borsuk-Białynicka et al. 1999: 183–184).

Material examined

Caudata: *Marmorerpeton oxoniensis* + Kirtlington "salamander A" (UCL collections), Middle Jurassic, and following recent taxa: *Ambystoma maculatum* ZPAL Ab. III/1; *A. macrodactylum*, series: UCMP 118864, 118863, 118865; *A. tigrinum* UCMP 138001 (adult + unnumbered immature); *A. t. californiensis* UCMP 118973 (immature + unnumbered adult); *A.t. melanostriatum* UCMP (unnumbered juvenile); *Andrias davidianus* ZPAL Ab.III/3 (juvenile); *Dicamptodon* sp. UCMP 118869 (larval); *Notophthalmus viridescens* UCMP 118873; *Paramesotriton chinensis* ZPAL Ab.III/7; *Plethodon jordani* UCMP 137921; *Salamandra salamandra* UCMP 118879; *Taricha torosa* ZPAL Ab.III/5; *Taricha* sp. UCMP 137900; *Tylotriton verrucosus* ZPAL Ab. III/14.

Salientia: *Triadobatrachus massinoti* MNHN, MAE 126, Early Triassic, and following recent taxa: *Bufo bufo* ZPAL Ab.III/9; *Pelobates fuscus* ZPAL Ab.III/6; *Rana esculenta* ZPAL Ab.III/10; *R. temporaria* ZPAL Ab.III/8; *Scaphiophus holbrooki* UCMP 118785.

Institutional abbreviations.—MNHN, Museum National d'Histoire Naturelle, Paris; UCL University College London, Department of Anatomy and Developmental Biology; UCMP, University of California, Museum of Paleontology, Berkeley; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Taxonomic background

One limitation of the present analysis is the lack of resolution with respect to the outgroup relationships of the Salientia, information that is basic for all decisions on character polarity (Maddison et al. 1984). The monophyly of the Lissamphibia including the Salientia, Caudata, and Gymnophiona was proposed by Parsons and Williams (1962, 1963), Szarski (1962), and Bolt (1969), and has been supported by many authors (e.g., Milner 1988; Rage and Janvier 1982; Gauthier et al. 1989; Trueb and Cloutier 1991; Cannatella and Hillis 1993; Ford and Cannatella 1993). However, it was rejected by Shishkin (1973) and has been questioned by others (e.g., Bolt and Lombard 1985). Amongst recent authors, Carroll has been one of the most consistent advocates of a polyphyletic origin of the Lissamphibia (Carroll and Holmes 1980; Carroll 1999; Carroll et al. 1999). According to this author, different patterns of skull fenestration (and thus adductor mandibulae muscles), suggest a very remote ancestry of the three groups collectively termed Lissamphibia (Carroll 1999). Moreover, Carroll et al. (1999) argue that anurans are the only lissamphibian group, which show a temnospondyl rate and sequence of ossification, whereas caudates and gymnophionans strongly differ in this respect. The latter share the ossification pattern of some lepospondyls, and a relationship to microsaurs has been postulated (Carroll et al. 1999). A sister-group relationship between caudates and salientians is here considered only as a possibility. It is not supported by any particular synapomorphy of the scapulocoracoid. However, our discussion relies heavily on caudates, because they afford unique data on the pattern of the cartilaginous parts of the pectoral girdle, considered basic for lower tetrapods. This pattern is particularly instructive as a model of the initial stage of development of the salientian structure, most probably resulting from paedomorphosis (Bolt 1977; Milner 1988; Roček and Rage 2000).

One relatively stable point in the discussion of lissamphibian affinities has been a temnospondyl, and more precisely dissorophoid, ancestry for the Salientia (whether or not as part of a monophyletic Lissamphibia) (Bolt 1969, 1977, 1991; Shishkin 1973; Bolt and Lombard 1985; Milner 1988, 1990, 1993; Daly 1994; Carroll 1999; but see Laurin and Reisz 1997; Laurin et al. 2000). However, scapulocoracoids are poorly known in dissorophoids (Carroll 1964; Gregory 1950; Milner 1982), so we have

used other temnospondyls and then additional lower tetrapod groups, as consecutive outgroups. Within the context of this paper, however, temnospondyl is used to mean non-lissamphibian temnospondyl, although this is not directly stated in each case.

The most recent hypotheses by Laurin and Reisz (1997), Laurin et al. (2000), and Yates and Warren (2000) that shift the ancestry of the lissamphibians to the lepospondyls, tend to focus on the peculiarities of the lepospondyl, and mainly microsaur, skeleton. However, it should be stressed that the structure of the scapulocoracoid is quite consistent throughout early tetrapods (beginning with stem tetrapods; Coates 1996; Lebedev and Coates 1995), allowing for some minor reductions and variability. For this reason, discussion of the polarity of scapulocoracoid character states is not strongly affected by the overall choice of tetrapod relationship hypothesis.

Amphibia Linnaeus, 1758

Salientia Laurenti, 1768

Czatkobatrachus Evans and Borsuk-Białynicka, 1998

Czatkobatrachus polonicus Evans and Borsuk-Białynicka, 1998

Holotype: ZPAL Ab IV/7.

New material.—The material includes seven specimens of the scapulocoracoid: ZPAL Ab-IV/ 0, 1, 26, 27, 28, 29, 30. Most specimens have the scapular region preserved, with only part of the glenoid. Only one specimen, ZPAL Ab IV/26, is almost complete.

Range.—Early Triassic of Poland.

Supplementary diagnosis.—Undivided scapulocoracoid with a poorly developed coracoid part. Glenoid large subcircular and facing laterally. Long scapular blade, very slender proximally. Supraglenoid foramen anterior to dorsal section of the glenoid.

Description.—The pectoral girdle of *Czatkobatrachus polonicus* is represented by an undivided scapulocoracoid. We consider that this was the only endochondral element of the pectoral girdle present in this genus, but the structure of the dermal parts of the girdle remains unknown. The scapulocoracoid consists of a subtriangular ventral plate and a narrow blade that widens distally to about twice the proximal width of the blade, although no specimen has the distal tip preserved. The axis of the scapular blade makes an angle of about 65° with the long axis of the ventral plate, so that the scapular blade sloped anteroventrally in life. The ventral plate faces laterally except for the posterior and ventral (thus coracoid) borders of the glenoid which form a narrow, medially curved strip at an angle of more than 90° (about 110°) to the scapula. Specimen ZPAL Ab-IV/26 shows a fairly straight ventral border of unfinished bone (Fig.1A, C) which indicates that it was originally continued in cartilage. Other specimens have the coracoid part unossified or broken away. The posteroventral region of the scapulocoracoid bears a large glenoid that occupies most of its surface and extends far posteriorly. What is here interpreted as a supraglenoid foramen is a subvertical cleft (Figs. 1A, 2, 3) situated anterior to the dorsal part of the glenoid. It partly separates the glenoid region of the scapula from the acromial part. The latter is a long, laterally (or slightly anterolaterally) flattened process extending ventrally from the scapula of which it constitutes an integral part. Ventral to the glenoid, the acromial process fuses with both the scapular part of the glenoid and the coracoid part from which it is separated by a rounded supracoracoid foramen (approx 0.3 mm in diameter). This foramen pierces the girdle anterior to the ventral margin of the glenoid (exactly where, in urodeles, the *incisura coracoidea* separates the procoracoid from the coracoid section of the scapulocoracoid, Fig. 6A, B). The foramen leads into a short canal directed toward the supraglenoid foramen. Both foramina open on the medial surface of the scapula (Fig. 1C) in the subscapular fossa. The glenoid is subcircular in outline, i.e. much deeper dorsoventrally than is usual in lower tetrapods, and is hemispherical rather than funnel shaped (in contrast to urodelans). A distinct anteroventral glenoid tubercle contributes a small articular surface to its anteroventral border (Fig. 1A).

As demonstrated by specimen ZPAL Ab-IV/29, the distal half of the scapular blade bears a longitudinal lateral groove running parallel to the posterior margin (Fig. 2A). This may be a trace of the contact between m. latissimus dorsi (posterior) and m. dorsalis scapulae (anterior). On the medial surface of the acromion, a sharp crest extending along the anterior margin, and a flattened anterolateral surface adjacent to this crest, were probably sites of origin of the deltoid muscle, a strong protractor of the humerus.

Dimensions.—In the best preserved scapulocoracoid ZPAL Ab-IV/ 26, the estimated length of the proximal part of the scapula is about 3.6 mm. The proximal width of the shaft is approx. 1 mm in the same specimen. The preserved length of the shaft (above the glenoid) is about 3 mm in the specimen ZPAL Ab IV/29 with dimensions closely similar to ZPAL Ab-IV/26, but lacking a ventral part (Fig. 2A). No further measurements can be made due to damage.

Attribution.—The specific attribution of disarticulated skeletal remains involves two problems: assignment of the bones to a single species (or even individual) and the identification of the animal concerned. The first may be accomplished in one of several ways: by matching articular surfaces, by matching surface texture (e.g., sculpture patterns or the unfinished bone pitting often associated with immature or paedomorphic taxa) or by comparing them against known articulated material of related taxa. The result is always conjectural. In the case of *Czatkobatrachus polonicus*, the bones represented can only rarely be fitted with one another directly (e.g., ulna and humerus). The Early Triassic Czatkowice assemblage is composed of thousands of bone
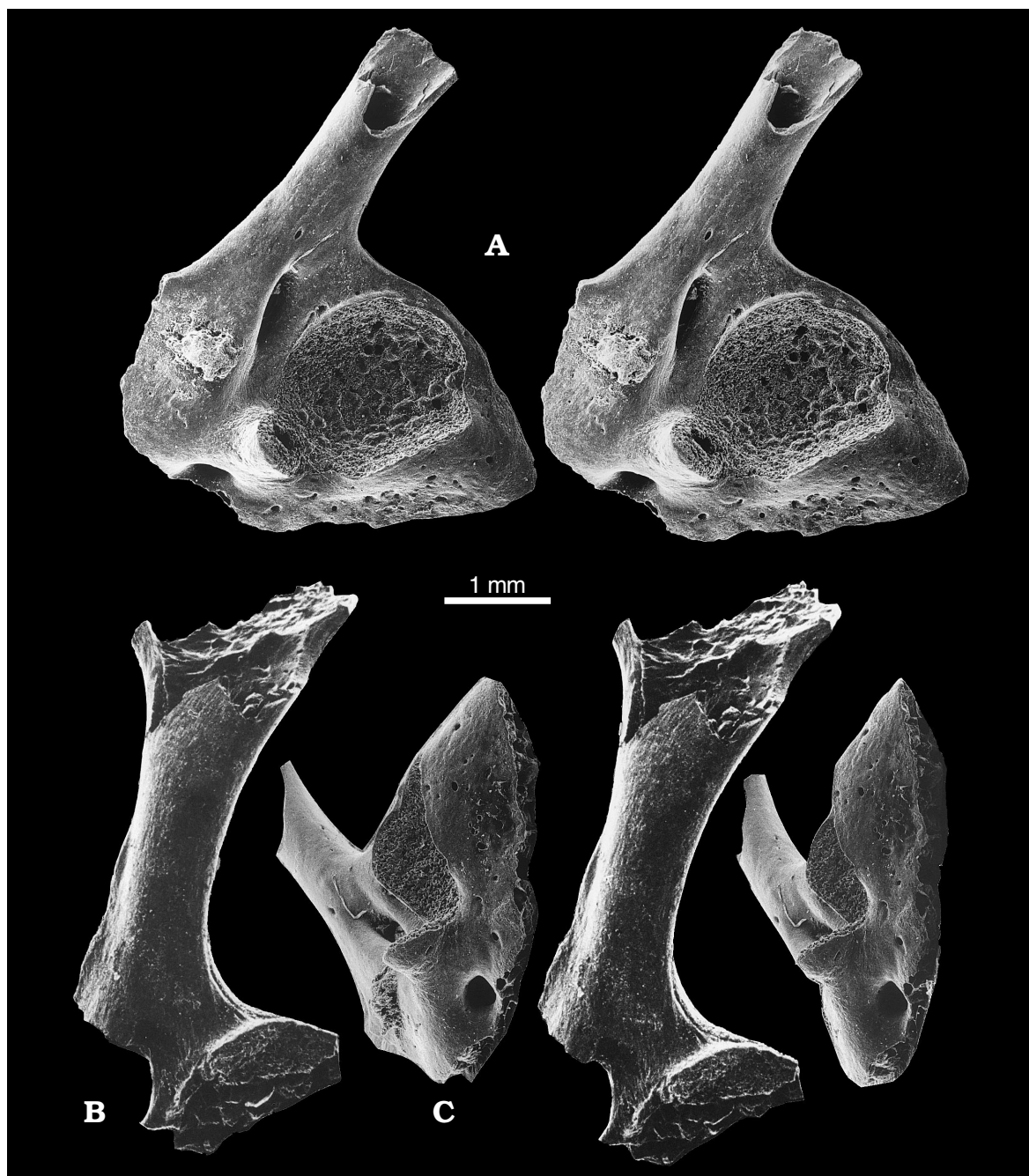
Fig. 1. *Czatkobatrachus polonicus* (Early Triassic). Left scapulocoracoid, ZPAL Ab IV/26. **A**. Lateral view. **C**. Ventral view. **B**. Scapular blade and fragment of glenoid, ZPAL Ab IV/28; lateral view. SEM stereo-micrographs.

fragments of different size (from about 1 to 20 mm). The *Czatkobatrachus* material belongs to the smallest sized fraction, usually not exceeding a few mm in length, and amounts to about 30 specimens. In addition, this fraction includes two tiny reptiles (possible lepidosauromorphs, Borsuk-Białynicka and Evans 1999), a few fishes and some fragmentary temnospondyls. The vertebrae, ilia and humeri on which the Polish pre-frog species has been founded (Evans and Borsuk-Białynicka 1998) are consistent in their frog-like aspect. An isolated caudal vertebra corresponding

in size and morphology to the presacral vertebrae, and differing from reptile vertebrae, and a separate ulna closely corresponding in size and shape to the distal humeral head, have been included. They appear to represent a primitive salientian stage of evolution, approximately the same as that of *Triadobatrachus massinoti* (Piveteau, 1936), a recognised stem-frog of almost the same Early Triassic age. The general resemblance between known elements of the Triassic taxa predicts that the morphology of currently unknown bones should be similar and intermediate between

Fig. 2. *Czatkobatrachus polonicus* (Early Triassic). Scapular part of the right scapulocoracoid. **A₁**. ZPAL Ab IV/29 in anterolateral view. **A₂** The same in lateral view. **B₁**. ZPAL Ab IV/27 in anterolateral view. **B₂**. The same in lateral view. SEM stereo-micrographs.

those of ancestral temnospondyls, and of anurans. The scapulocoracoid herein assigned to *Czatkobatrachus polonicus* fits this pattern. Its attribution is supported by its relative size compared to that of the holotype ilium and other referred material (Evans and Borsuk-Białynicka 1998), and by the relative frequency of individual *Czatkobatrachus* bones within the assemblage (Borsuk-Białynicka et al. 1999). The finished texture of the bone surface indicates that the bones are adult (in contrast to the bone texture of juvenile temnospondyl material in the deposit) and there is nothing to support attribution of the scapulocoracoids described herein to any of the temnospondyls represented within the Czatkowice assemblage.

Character analysis

Scapula shape and the orientation of the scapular axis. —Like many primitive tetrapods, *Czatkobatrachus* shows an anteroventral slope of the main axis of the scapula (Figs. 1A, 2A), due originally to the primitive position of the cleithrum, and a posterior extension of the glenoid part of the scapulocoracoid (e.g., Clack 1987; Coates 1996: 381; Holmes *et al.* 1998; Meckert 1993; compare cleithrum position in *Ichthyostega*, see Jarvik 1996). This character is thus considered plesiomorphic in *Czatkobatrachus* although the absence of any facetting along the anterior scapula margin (Fig. 2A)
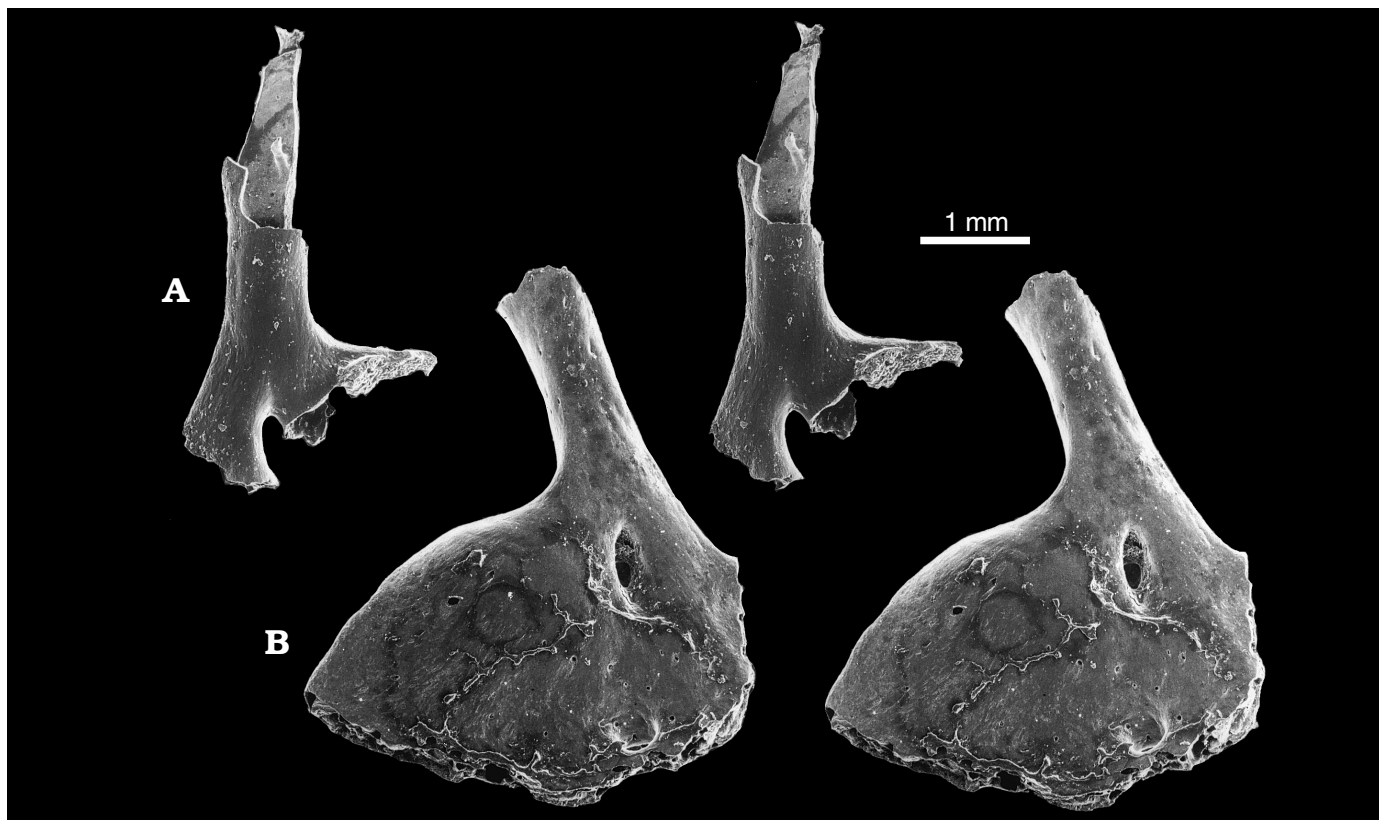
Fig. 3. *Czatkobatrachus polonicus* (Early Triassic). **A**. Left scapula ZPAL Ab IV/1 in lateral view. **B**. Left scapulocoracoid ZPAL Ab IV/26 in medial view. SEM stereo-micrographs.

shows that a primitive cleithral pattern was not retained. However, the scapular blade is decidedly more slender in *Czatkobatrachus* (Fig. 4C) than in any temnospondyl (Fig. 4A, B). Among temnospondyls, only some dissorophids (Gregory 1950; DeMar 1968) have a comparatively long and narrow scapular blade which may be correlated with their terrestrial habits. In extant amphibians, the shape and inclination of the scapular blade are much more variable and more clearly dependent on the way of life. Anurans typically have a subquadrangular scapula that is more or less enlarged proximally and distally with a subvertical scapular axis (Fig. 9A, D, E). The details of the anuran scapula are difficult to interpret in terms of phylogeny, but seem to be derived in many ways (Duellman and Trueb 1986: figs. 13–36) as is the whole pectoral girdle. In contrast, the overall shape and inclination of the scapula of *Czatkobatrachus* has not departed from the temnospondyl type by much (Fig. 4C).

The number of ossification centres and subdivision of the scapulocoracoid.—In anamniote tetrapods generally, the scapulocoracoid is thought to develop from a single scapular ossification centre (e.g., temnospondyls Holmes et al. 1998: 70; Warren and Snell 1991: 52; Meckert 1993; microsaurs Carroll and Gaskill 1978). Subdivision of the scapulocoracoid is unknown in dissorophoids (*Doleserpeton*, *Amphibamus*, *Trematops*, Milner 1988). Most informative are scapulocoracoids of the stem tetrapods, e.g., *Ichthyostega* (Jarvik 1996: 58), *Acanthostega* (Coates 1996), *Tulerpeton*

(Lebedev and Coates 1995), that display a single element pattern, thus considered plesiomorphic within the tetrapods. The plesiomorphic state appears to be shared by *Czatkobatrachus polonicus* (Fig. 11) as well as by some anthracosaurs, e.g., *Proterogyrinus* (Holmes 1980: 355). Two ossification centres that occur in a number of other anthracosaurs including the very early, Lower Carboniferous stem-anthracosaur *Whatcheeria* (Lombard and Bolt 1995), both *Seymouria* (Fig. 5A) and *Diadectes* (Goodrich 1930: 174) and *Discosauriscus* (Klembara and Bartic 2000), are considered derived. Likewise, the partition of the single ossification centre demonstrated in some temnospondyls by Schoch (1999) (Fig. 5B) may be considered derived, but is clearly in parallel to that of distantly related anthracosaurs. In the Urodela, the number of ossification centres is variable. One centre seems to prevail in Cryptobranchidae, Prosirenidae, Proteidae, Ambystomatidae, and most Salamandridae (Nauck 1967), and this appears to be the primitive condition since it also occurs in the primitive karaurid caudate *Marmorerpeton* (Evans personal observation). Two centres occur in the Sirenidae and Amphiumidae (Duellman and Trueb 1986: fig. 17-1), while *Salamandra* and *Triturus* (Salamandridae) display three ossification centres (Nauck 1967). However, independent of the number of centres, the urodelan scapulocoracoid is usually subdivided into three parts by incisions in its rim (Fig. 6). The *incisura coracoidea* (Fürbringer 1874 *fide* Nauck 1967) in the anteroventral margin, is the main

Fig. 4. Fossil amphibian scapulocoracoids in left lateral view. **A**. *Sclerocephalus haeuseri* (Permian) after Meckert 1993: fig. 2A (more or less the same type as *Dendrerpeton acadianum*, Middle Carboniferous, after Holmes et al. 1998: fig. 7A). **B**. *Dissorophus multicinctus* (Permian) after DeMar (1968). **C**. *Czatkobatrachus polonicus* (Early Triassic) ZPAL Ab IV/26.
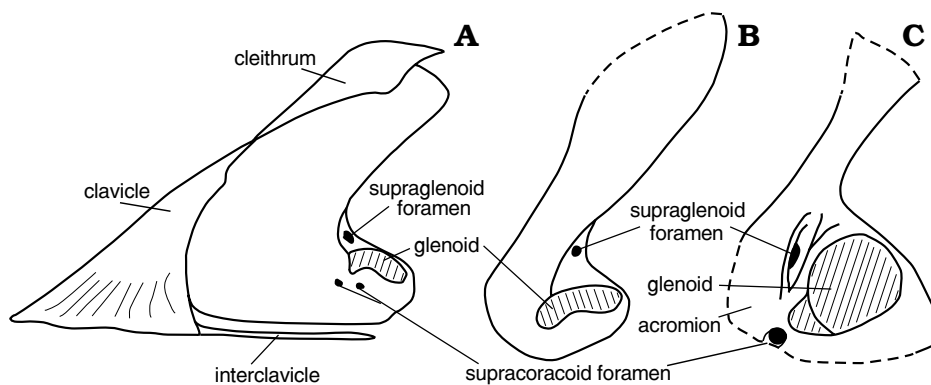
landmark. It may close in ontogeny to leave a *foramen diazonale* (Nauck 1967) that gives passage to the supracoracoid nerve and blood vessels, becoming the supracoracoid foramen in a fully ossified adult element. The *incisura coracoidea* separates the coracoid from the so-called procoracoid (homologous to the acromion of the lower tetrapods according to Gegenbaur 1865, *fide* Nauck 1967, but not precisely so according to Nauck 1967, being an intermediate region between the scapula and coracoid). Another incision separates the procoracoid from the scapula. Urodela apparently preserve a juvenile scapulocoracoid morphology consistent with the paedomorphosis that is widely accepted as a principal factor in the evolution of lissamphibians (Milner 1988). This pattern is compatible with the hypothesis (as shown by Janvier's 1980: fig. 9.5, and not by fig. 9.3) that the scapulocoracoid developed from a fusion of the distal expansions of the three buttresses of the osteolepiform girdle (Fig. 7A), supported by the tripartition of the scapulocoracoid plate in the Panderichthyida (Janvier 1998: 225). Perhaps, in early tetrapods the three cartilaginous parts fused early in ontogeny, with ossification typically proceeding in one plate. In some terrestrial anthracosaurs (Anthracosauria *sensu* Laurin et al. 2000), ossification must have been accelerated and proceeded in more than one part (scapula and coracoid, *Seymouria* and *Diadectes*; scapula and two coracoids in parareptiles and pelycosaurs Romer 1956). The same occasionally occured in derived temnospondyls (see above), but given their generally more aquatic habits, a retardation in the fusion of cartilaginous parts apparently occured more frequently. The preservation of the threefold pattern in anurans (Figs. 9, 10), might also have resulted from heterochrony. In this case, the shape of the girdle elements has been further transformed in connection with requirements of locomotion.

In *Czatkobatrachus* (Fig. 1), the anteroventral part of the scapulocoracoid is separated from the coracoid by a large supracoracoid foramen situated close to the unfinished margin of the bone in the urodelan style. This anteroventral part thus corresponds to the procoracoid region of urodeles. At the same time, it is intimately fused to the scapula as its acromial part, except in the region where it is separated from the glenoid by a deep supraglenoid fissure (see below) extending from the supraglenoid foramen down to the supra-

coracoid one. In *Leiopelma* and the Jurassic *Notobatrachus* (Baez and Basso 1996) it is the scapular cleft that separates the two parts (Fig. 9D, E). However, in *Czatkobatrachus*, the scapulocoracoid reveals another more basic subdivision. The supraglenoid fissure follows the border between the posteromedial buttress of basal tetrapods, bearing the glenoid, and the anterolateral scapular blade (the acromion of basal tetrapods), homologized here with the procoracoid of urodeles. Changes in forelimb position and usage will directly affect the size, and orientation of the buttress.

Extent and shape of the coracoid region.—In stem tetrapods and in many other Paleozoic anamniotes (e.g., Romer 1957; DeMar 1968; Meckert 1993; Holmes et al. 1998), the
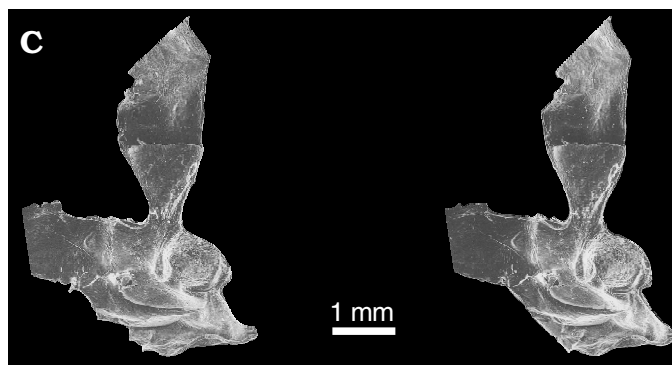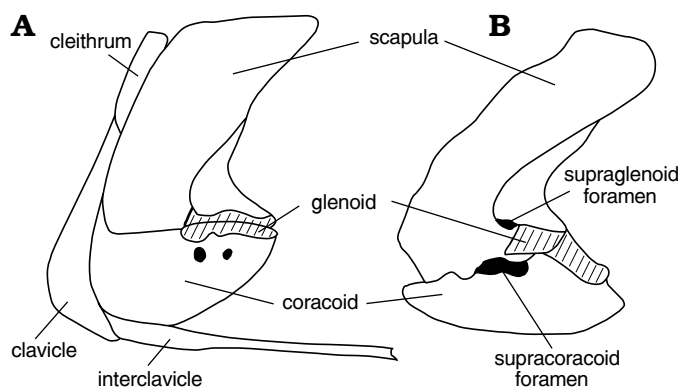

Fig. 5. **A**. *Seymouria* sp. (Early Permian) after Romer (1956: fig. 143). **B**. *Mastodonsaurus giganteus* (Middle Triassic) after Schoch (1999: fig. 40). **C**. *Ambystoma maculatum* (Recent) ZPAL Ab III/1. Left scapulocoracoid in lateral view. SEM stereo-micrographs.
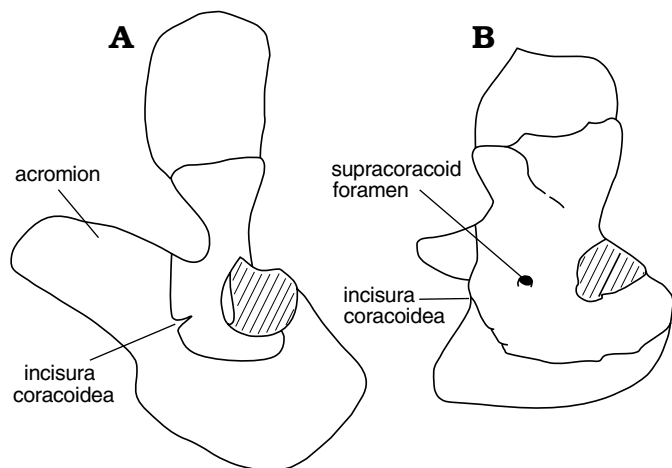
Fig. 6. Tetrapod pectoral girdles in left side view. Not to scale. **A**. *Ambystoma maculatum* (Recent) ZPAL Ab III/1. **B**. *Taricha torosa* (Recent) ZPAL Ab III /5.

coracoid region usually formed a transversely narrow plate of unfinished bone ventral to the glenoid (Jarvik 1996; Coates 1996). This state, considered plesiomorphic, is shared by *Czatkobatrachus* (Fig. 1A, C). In some Triassic temnospondyls (e.g., Bystrov and Efremov 1940; Warren and Hutchinson 1990; Nikitin 1997a), the coracoid has been totally reduced (Fig. 8). In contrast, the ventral extension and bar-like shape of the anuran coracoid (Figs. 9A, D–F, 10), as well as its separation from the procoracoid by a wide space (*scaphoid fenestra* sensu Nauck 1976) corresponding to the *incisura coracoidea* and including the supracoracoid foramen, are novel and should be considered autapomorphic for this clade. The coracoid of the Early Jurassic frog *Vieraella herbstii* (Fig. 9B), as figured by Estes and Reig (1973) and Baez and Basso (1996), was apparently still plate-like, but shortened in its parasagittal axis. This seems to be a primitive condition, but the state of preservation of this single specimen does not permit detailed discussion. The coracoid of the Middle Jurassic *Notobatrachus* (Fig. 9D), as reconstructed by Estes and Reig (1973), shows a more derived condition, being deeply incised proximally to include the supracoracoid foramen. In this genus, unlike *Vieraella*, the proximal part of the coracoid appears to be reduced to a narrow peduncle bearing the ventral glenoid surface, whereas the distal part remains expanded and primitively flattened. A similar condition is preserved in the extant *Leiopelma* (Fig. 9E).

Glenoid outline.—The low, elongated strap-like or screw-shaped glenoid (Figs. 4A, B, 5, 7B) of stem tetrapods (e.g., *Acanthostega* Coates 1996), temnospondyls (Miner 1925; Nikitin 1997a) and anthracosaurs (Holmes 1980) is considered plesiomorphic. The elongated, subquadrangular, longitudinally concave glenoid of the Microsauria, as best illustrated by Carroll and Gaskill (1978: figs. 27A, 90B) in *Pantylus* and *Hyloplesion*, seems to be another version of the same thing. In contrast, the glenoid of *Czatkobatrachus* (Figs. 1A, 4A) is very large, subcircular and evenly concave.

In shape and position, it is most reminiscent of that of some urodelans (see e.g., Fig. 6), while differing from the most common urodelan type in some details (hemispherical in *Czatkobatrachus*, more funnel-shaped in urodelans) and in orientation (see below). It is considered derived. It also shares its circular outline with the Anura (while differing in orientation, see below). However, these qualities of the glenoid must have evolved in parallel in the Salientia and Caudata, because the strap-like shape of the glenoid in basal karaurid caudates such as *Marmorerpeton* (Evans, work in progress) is closely similar to that of archaic tetrapods.

The orientation of the humerus perpendicular to the body axis, illustrated by Jenkins and Shubin (1998: fig. 6A) as a primitive tetrapod condition, represents the abducted position of the limb. It operated in the horizonal plane through the posterolateral quarter of a circle to attain a position parallel to the body wall at the completion of the stride (Miner 1925; see Nikitin 1997a for different interpretation). According to Kuznetsov (1995), this motion was accomplished at least partly by a rotation of the scapulocoracoid around its vertical axis, as occurs in living urodeles (e.g., Evans 1946) and many other tetrapods. Nikitin (1997a: 75) considered that the horizontal orientation and limited height of the primitive glenoid was a condition enabling vertical mobility of the humerus at the joint. However, the restriction of an articular surface in a certain direction is more likely to indicate a limitation rather than an intensification of mobility in that direction. The dorsal increase in the diameter of the glenoid in *Czatkobatrachus* probably enhanced vertical movements of the humerus as it does in the case of the semicircular glenoid of urodeles. According to Evans (1946), increased vertical mobility is important during the phase of slow gait in salamanders when the body is raised clear of the ground and the anterior legs are used in weight bearing. It should be still more important for shock absorption in frogs, and may represent a preadaptation for the derived jumping locomotion of crown-group taxa.

Glenoid orientation.—According to Janvier (1980) the glenoid fossa of choanate fishes faces backwards (Fig. 7A₁) and slightly laterally, turning laterally or slightly posterolaterally in early tetrapods. However, there is some variation. The orientation seems posterior in *Ichthyostega* (Jarvik 1996) (Fig. 7B₁), more lateral in *Acanthostega* (Coates 1996), and slightly posterolateral in *Tulerpeton* (Lebedev and Coates 1995) and *Eryops* (Miner 1925). It is lateral in *Proterogyrinus* (Holmes 1980, 1984) and *Greerpeton* (Godfrey 1989), and variable in microsaurs (Carroll and Gaskill 1978). This variability is a function of the changing position of the humerus, and of the forelimb as a whole, in the early stage of terrestriality.

An overall trend from a plesiomorphic posterolateral position to a more derived lateral one seems to be unequivocal within early stages of tetrapod phylogeny, but the trend is often reversed in more modern lineages. The directly lateral position of the glenoid in *Czatkobatrachus* (Fig. 1A) is clearly derived by comparison with dissorophids, under the assump-
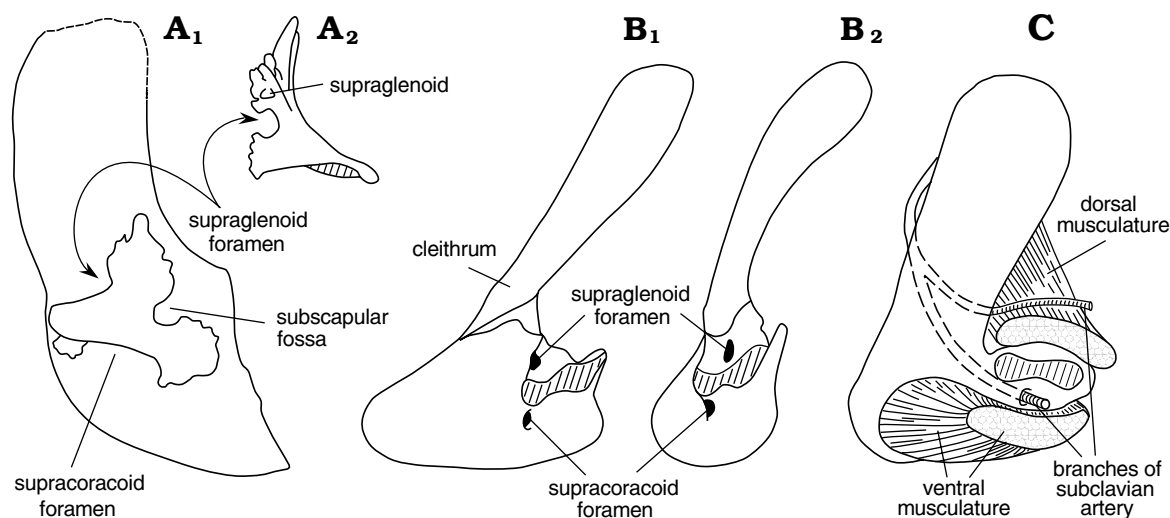
Fig. 7. Fish and early tetrapod scapulocoracoids. Not to scale. **A**. Osteolepid fish type (gen. et sp. indet.) in medial (A$_1$) and posterior (A$_2$) view; both after Janvier (1980: fig. 2). **B**. Basal tetrapod type in left side view (B$_1$), and in posterior view (B$_2$); both after *Ichthyostega* (Late Devonian) figures by Jarvik (1996: fig. 42). **C**. Temnospondyl type with muscles and neurovascular structures partly reconstructed; after Janvier (1980: fig. 10).

tion that the posterolateral orientation of the glenoid in *Dissorophus multicinctus* (DeMar 1968) is typical of the group, and that dissorophids may be used as an out-group for the Salientia. Consequently, the lateral orientation would either be autapomorphic for *Czatkobatrachus* or synapomorphic for the Salientia. In the latter case, the posterior position of the typical anuran glenoid (Fig. 11.8) would represent an evolutionary reversal. This possibility is considered below (see Discussion). According to our observations, the glenoid position of Urodela is a little more posterior than that of *Czatkobatrachus* and more lateral than in living frogs, but probably more variable than this.

The supraglenoid foramen: homology, position, and closure.—The scapulocoracoid of primitive tetrapods is perforated by two main foramina, one above and one below the level of the glenoid fossa (Fig. 7B). It is generally accepted that these foramina gave passage to major branches of the brachial plexus (the diazonal nerve of Goodrich 1930) and accompanying blood vessels, with the upper (supraglenoid foramen) supplying the dorsal (extensor) muscles (e.g., M. dorsalis scapulae, m. latissimus dorsi) and the lower (supracoracoid foramen) carrying branches to the ventral (flexor) series (e.g., m. pectoralis) (Goodrich 1930; Romer 1956). This interpretation is based mainly on presumed homologies between fish and primitive tetrapods (Fig. 7C, Janvier 1980), because one or both of the foramina often disappear in more derived groups (see below).

The homology of the supraglenoid foramen of primitive tetrapods and the scapular cleft in frogs.—In lower tetrapods, the supraglenoid foramen is typically positioned towards the posterior margin of the scapula (e.g., Miner 1925; DeMar 1968; Holmes 1980; Holmes et al. 1998; Carroll and Gaskill 1978). The scapular blade makes up the anterolateral border of the foramen while the supraglenoid buttress forms the

posteromedial one, a situation directly comparable with that of osteolepiform fishes (Jarvik 1980; Janvier 1980). This position is considered plesiomorphic within tetrapods. In contrast to that of other tetrapods, the foramen of *Czatkobatrachus* is situated in a vertical cleft directed towards the supracoracoid foramen. This cleft partly divides the bone into a posterior "glenoid" (buttress) part and an anterior procoracoid or acromial one, producing an incipiently bifid appearance that resembles the cleft type scapula of anurans (Fig. 9). On this basis, the supraglenoid foramen would be considered homologous to the anuran cleft (as Goodrich 1930, implied: 177), and the cleft scapula is synapomorphic for Anura as a whole. This conclusion would be in contrast to the opinion of many workers (e.g., Kluge and Farris 1969; Trueb 1973; Lynch 1973; Duellman and Trueb 1986: 346) that a short uncleft scapula was the basal anuran condition, but is in agreement with the view of Estes and Reig (1973). The cleft scapulae of the Middle Jurassic frog *Notobatrachus* (Estes and Reig 1973; Baez and Basso 1996: fig. 10D), and that of some species of the extant primitive frog *Leiopelma* (Fig. 9E herein) are thus considered plesiomorphic. The structure of the scapulocoracoid of the Early Jurassic frog *Prosalirus bitis*, as illustrated by Jenkins and Shubin (1998: fig. 5B, see Fig. 9F herein) also suggests a basically *Notobatrachus*-like structure, as does that of the Middle Jurassic *Eodiscoglossus oxoniensis* from Britain (Evans et al. 1990). The condition in the Early Jurassic *Vieraella* is unfortunately unknown (Baez and Basso 1996: 138). The Late Jurassic pipoid, *Rhadinosteus* (Henrici 1998), from the Morrison Formation of the USA, displays a relatively long, cleft scapula, suggesting that the short uncleft scapulae of later pipoids (Sanchiz 1998) are also secondary rather than primitive. In this context the uncleft scapula of one of the most primitive extant frogs, *Ascaphus* (Ritland 1955), should also be considered derived. As a demonstration of homology, it would be useful if the
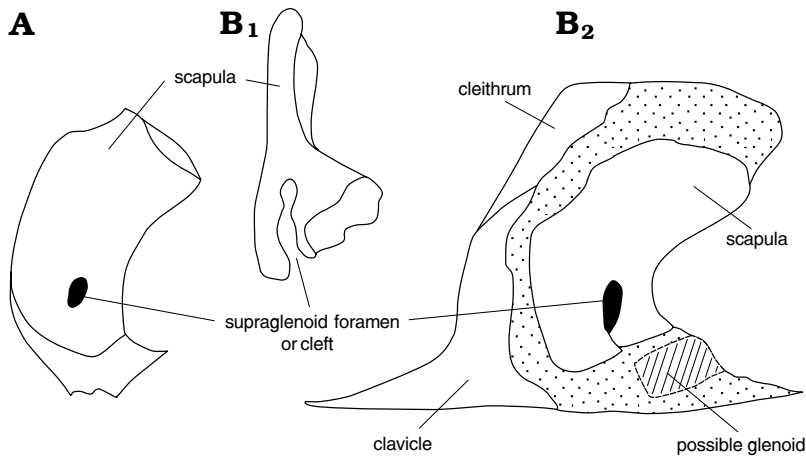
Fig. 8. Reduced ossification in temnospondyl scapulo-coracoids. **A**. *Dvinosaurus primus* (Late Permian) after Nikitin (1997b) in left lateral view. **B**. Scapula of *Benthosuchus sushkini* (earliest Triassic) in posterior view (B$_1$). The same in left lateral view with reconstructed cartilaginous and dermal bone parts of the girdle (B$_2$). Both after Bystrov and Efremov (1940: figs. 47C and 49 respectively). Not to scale.

anuran scapular cleft could be shown to convey nerves and blood vessels to the dorsal limb muscles, as hypothesised for extinct taxa. Unfortunately, according to de Vos (1938: 68), the anuran cleft houses only a fold of the synovial membrane of the joint and permits greater movements of the humeral head within the glenoid cavity during locomotion. This suggestion is supported by dissections of modern frogs (observations by MBB on *Rana*, SEE on *Xenopus* and by Dr. Z. Roček on *Rana* personal communication).

A proximally split scapula also occurs in some temnospondyls (Warren and Snell 1991). According to the latter authors, there are actually two distinct types of scapulocoracoid in this group. The first has a comparatively small supraglenoid foramen (Figs. 4A, B, 7B), lying dorsal to the glenoid and between the blade and the supraglenoid buttress. The second, more derived, type has the foramen open proximally so that the scapula is separated from the supraglenoid buttress by an incision, and thus the proximal end of the scapula
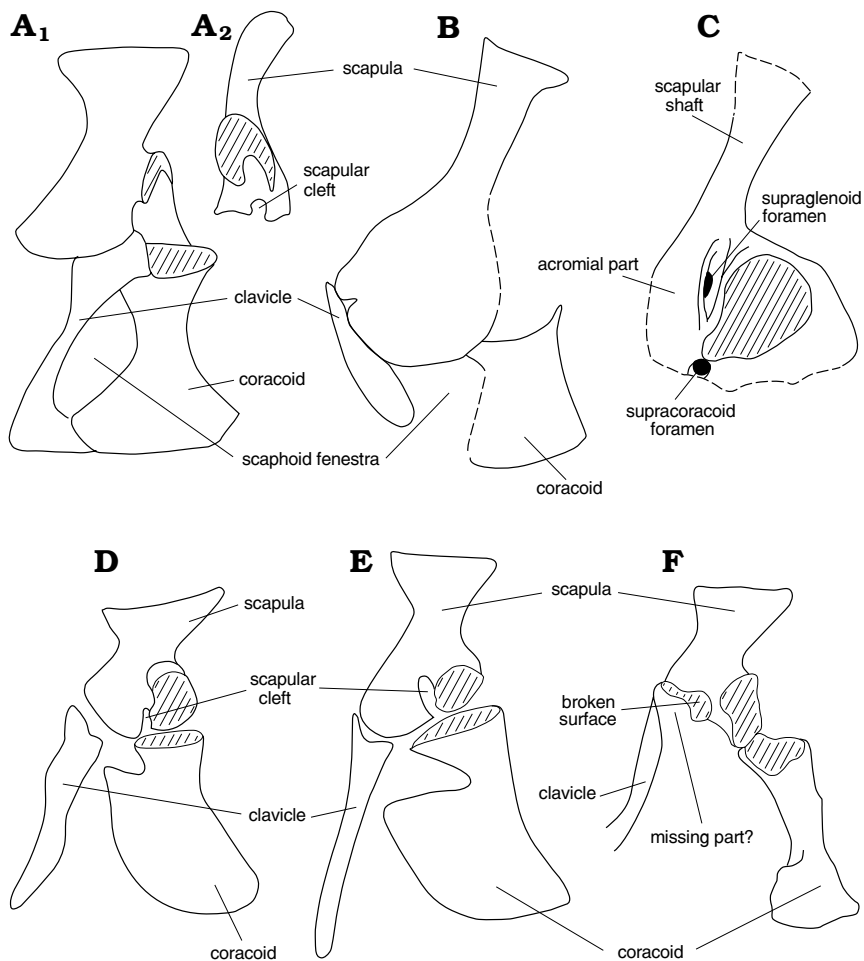

Fig. 9. Pectoral girdles of different salientians. **A**. *Rana temporaria* (Recent) ZPAL Ab.III/8. **B**. *Vieraella herbsti* (Early Jurassic) after Baez and Basso (1996). **C**. *Czatkobatrachus polonicus* (Early Triassic) ZPAL Ab IV/26. **D**. *Notobatrachus degiustoi* (Middle Jurassic) after Estes and Reig (1973: figs. 1–7). **E**. *Leiopelma hamiltoni* (Recent) after Estes and Reig (1973: figs. 1–7). **F**. *Prosalirus bitis* (Early Jurassic) after Jenkins and Shubin (1998: fig. 5B reversed). Not to scale. All but A$_2$ in left lateral view, A$_2$ in posterior view.

Fig. 10. Left pectoral girdle of *Pelobates fuscus* (Recent) ZPAL. Ab III/6 in lateral (**A**) and posterior (**B**) view. SEM stereo-micrographs.

is bifid (Fig. 8B₁). An ontogenetic series of scapulocoracoids of *Benthosuchus sushkini* (Bystrov and Efremov 1940: fig. 67) shows that the incision of the second type of scapulocoracoid did not close during development, and thus the difference between the two morphological types is not a growth phenomenon (Warren and Snell 1991). The reduction in ossification seen in the second type is likely to be associated with an aquatic lifestyle.

Supraglenoid foramen position.—In those taxa in which the supraglenoid foramen is retained, its presence, size, and position vary considerably. There are several potential explanations for this, of which two seem more plausible. One obvious possibility is a change in the positional relationship between the scapulocoracoid and the nerves and blood vessels of the shoulder region (see below). However, foramen position may also have shifted as a consequence of unrelated morphological changes reflecting varying functional demands. Since the foramen typically emerges between the scapular blade and the margin of the supraglenoid buttress, any anterior expansion of this buttress could affect the position of the foramen. The function of the buttress is to accommodate compressive forces acting via the glenoid from the humeral head. Any change in position of the shoulder joint will therefore modify the trajectory of the forces generated, and thus the structure of the buttress and of the bone as a whole. In this way, shifts in the position of the supraglenoid foramen (e.g. Fig. 8A, see also Romer 1922: 547 for other examples) could be related to changes in limb position. For this

reason, the position of the foramen anterior to the dorsal part of the glenoid in *Czatkobatrachus* may result from its anterolateral migration in association with a lateral shift of the limb, with a concomittant apparent displacement ventrally in relation to glenoid, due to the increase in the vertical diameter of the latter. The scapular cleft in frogs also shows variation. The best known early frog scapulocoracoid is that of the Middle Jurassic frog *Notobatrachus degiustoi*, where the scapular cleft appears to have been visible on the lateral face of the scapula (Fig. 9D, see also Baez and Basso 1996: fig. 11) instead of being hidden in lateral view, as is usual in modern frogs (e.g., *Rana, Bufo, Pelobates*, Fig. 10). In the latter case the "glenoid" (buttress) part of the scapula is situated deep, medial to the acromial part, with the latter shifted posteriad to a more lateral plane (Fig 10).

According to Baez and Basso (1996: 144), the acromial part of the glenoid in *Notobatrachus* may have projected laterally with respect to the scapular part, but had probably not overgrown it to produce a lateral wall to the glenoid cavity. A similar lateral-type cleft is retained in most species of the primitive extant frog, *Leiopelma* (Fig. 9E), and the same may have been true in the case of the Early Jurassic *Prosalirus*. As shown by Jenkins and Shubin (1998: fig. 5B), the glenoid of *Prosalirus* is probably not complete, but the outlines of the proximal part of the scapula and of the peduncle of the scapular part of the glenoid both suggest a lateral orientation of the cleft (Fig. 9F). In addition, the overall shape of the scapula, and its articular surface, both resemble the laterally clefted
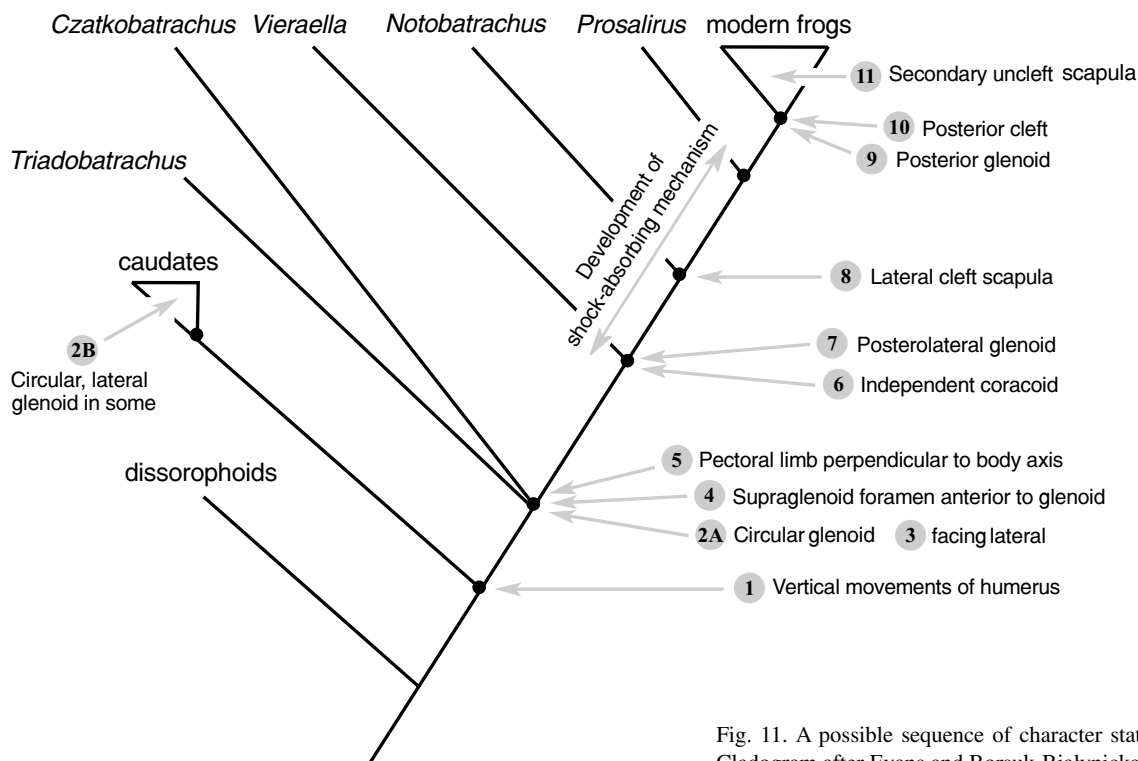
Fig. 11. A possible sequence of character states in salientian phylogeny. Cladogram after Evans and Borsuk-Białynicka (1998).

scapula of *Notobatrachus degiustoi* (Fig. 9D), although *Prosalirus* is probably more derived in showing a slightly more posterior position of the glenoid surface. Thus both *Notobatrachus* and *Prosalirus* support the existence of an evolutionary stage in the basal salientian phylogeny where the glenoid, and thus the cleft, retained a more lateral orientation. This, in turn, may have been related to limb position (see below).

Closure or change of function of the supraglenoid foramen.—As noted above, living urodeles lack a supraglenoid foramen while in frogs there is no structure passing through the scapular cleft (de Vos 1938). The arteria subclavia, that supplies blood to both sides of the limb, and the venae subscapularis and brachialis draining the limb pass posterior to the scapula (Gaupp 1896; Miner 1925; Miller 1934). The trunks and branches of the brachial plexus take the same route, with the nerve to the m. dorsalis scapulae winding around from the posterior margin of the scapula deep to the muscle. According to de Vos (1938), the anuran scapular cleft contains only a fold of the synovial membrane of the joint and is arranged to permit greater movements of the humeral head within the glenoid cavity during locomotion. This raises questions as to why the foramen lost its function in the transmission of neurovascular structures in living urodeles and frogs. The present course of the brachial neurovascular bundle in living lissamphibians suggests a posterior shift in the position of this bundle in relation to the pectoral girdle or an anterior migration of the latter. The retention of the supra-

glenoid foramen in basal salientians (*Czatkobatrachus*) and caudates (*Marmorerpeton*, Kirtlington "salamander A", Evans personal observation) shows that at least some part of the primitive neurovascular arrangement existed in the ancestry of lissamphibians, with loss of the foramen occuring independently in each lineage. One possible explanation for this might be changes that occured in the composition of the brachial plexus, and the position of the pectoral girdle, with the shortening of the lissamphibian axial skeleton and the reduction of the numbers of participating spinal nerve roots (Deuchar 1975; Duellman and Trueb 1986; Burke et al. 1995; Richardson et al. 1998).

Discussion

In primitive tetrapods, the humerus is generally thought to have moved in a horizontal plane through a posterolateral arc, with the proximal head moving over a low, horizontal, but screw-shaped glenoid surface (see p. 86). As in most living taxa, the range of forelimb motion was probably increased by rotation of the girdle (Kuznetsov 1995) in relation to the axial skeleton. This type of locomotion was apparently preserved in dissorophoids (DeMar 1968; Carroll 1964).

Assuming monophyly of the Lissamphibia, an increased mobility of the humerus in a vertical plane (Fig. 11.1), manifested by a vertical expansion of the glenoid (see p. 86),
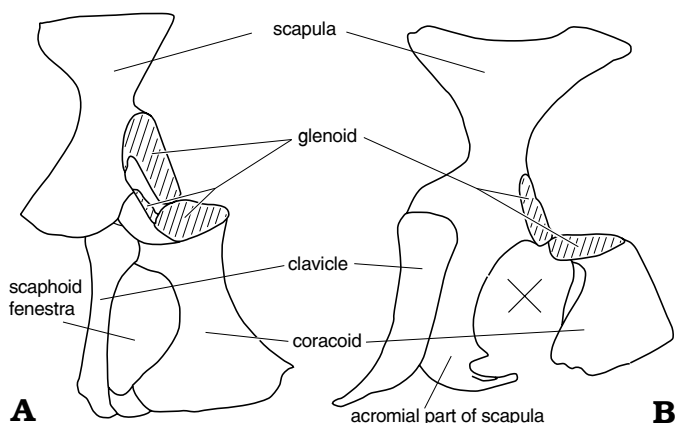
Fig. 12. Left pectoral girdle in lateral view. Not to scale. **A**. *Rana esculenta* (Recent) ZPAL. Ab III/10. **B**. Reconstruction of *Triadobatrachus massinoti* (Early Triassic) according to crown-group frog pattern with the ventral gap (denoted by X) interpreted as the scaphoid fenestra. Based on Rage and Roček (1989: fig. 2B), compiled from both sides. The clavicle turned clock-wise to put the wider end proximally as in Rage and Roček.

might be regarded as a synapomorphy of caudates and salientians. However, the resultant high glenoid of both groups differs in details of shape, and it is not shared by the most primitive caudates (Evans, work in progress). This feature has, therefore, probably evolved in parallel in the two groups (Fig. 11.2A, 2B), presumably as a result of similar early functional demands.

Based on the above discussion, a laterally facing glenoid (Fig. 11.3) and a supraglenoid foramen positioned anterior to the glenoid (Fig. 11.4), are tentatively considered as synapomorphies of the Salientia. The relative anterolateral shift of the supraglenoid foramen, as a prerequisite for its transformation into the lateral cleft, probably occured with a change in limb position. A lateral shift from the primitive half-adducted resting position of the forelimb to a more derived one perpendicular to the body axis (Fig. 11.5), is here regarded as correlated with a decrease in importance of this limb in propulsion, and an increased role in static functions (body-elevation, protection of body equilibrium, and shock-absorption (see p. 86). These functions are best executed with widely extended limbs. A steady lateral position of these limbs may have been of importance at the *Czatkobatrachus* stage of evolution given the absence of a sophisticated shock-absorption mechanism. We suggest that the subsequent modification of the coracoid into a bony strut signalled the appearance of the specialised anuran system whereby thrust is transmitted from the glenoid to the sagittal plane via two medially diverging prongs (coracoid and clavicle) (Emerson 1983). This may, in turn, have reduced the importance of forelimb position, thus allowing for reorientation of humerus and glenoid to permit movements in sub-para-sagittal plane. This reorientation resulted from the postero-lateral expansion of the acromial region over the glenoid, followed by the development of an articular surface on the posterior face of the former. The corresponding states of glenoid

and coracoid (Fig. 11.6, 7) are here considered as synapomorphies of crown-group frogs. We also suggest that the laterally growing acromial part displaced the supraglenoid foramen towards the glenoid (without initially changing its lateral position), to produce the lateral cleft stage that appears basal to crown-group frogs (Figs. 9D, E, 10.8). Continued posterior expansion of the acromial part resulted in a more posterior orientation of the glenoid and cleft (Figs. $9A_2$, 10, 11.9, 11.10). This in turn brought the humerus axis closer to the body in modern frogs, a position of greater advantage in the initial phase of the jump (e.g. in push-off and in controlling anterior body orientation, Jenkins and Shubin 1998).

The basal anuran stage is most clearly seen in the Jurassic *Notobatrachus* (Baez and Basso 1996: 144), where the coracoid had already been reduced to a peduncle proximally (Fig. 9D), while remaining strongly expanded distally. It had clearly developed an ossification centre of its own (Fig. 11.6), and had lost contact with the procoracoid from which it is separated by a large space (scaphoid fenestra) including the supracoracoid foramen (Goodrich 1930). The transformation of the supraglenoid foramen into the scapular cleft may have been prompted by the requirements of the developing shock-absorption mechanism, in which the coracoid, procoracoid and clavicle diverged in the direction of the sagittal axis of the ventral side of the body. A divergence of the glenoid (buttress) and acromial parts should have helped to brace the two ventral prongs of the girdle.

The pectoral girdle of *Triadobatrachus* and *Vieraella*

Given the lack of articulated skeletons of *Czatkobatrachus* (Evans and Borsuk-Białynicka 1998), it would be useful if the structure of its pectoral girdle proved to be similar to that in *Triadobatrachus*, a stem-salientian of approximately the same age and evolutionary stage known from the whole skeleton. However, the pectoral girdle of the holotype and only specimen of *Triadobatrachus* (MNHN MAE 126), most recently reviewed by Rage and Roček (1988) and Roček and Rage (2000), has been damaged and is difficult to reconstruct. Rage and Roček interpreted the coracoids as separate ossifications, and their reconstruction (1989: fig. 5, p. 15) suggests a basically anuran condition with the clavicle/procoracoid and coracoid ossifications separated by a ventromedial gap (denoted by X in Figs. 12 to 14). Such a difference between *Triadobatrachus* and *Czatkobatrachus* would be surprising. Besides, if the ventromedial gap were to be considered as a scaphoid fenestra, the procoracoid part would be an extremely long ventral prolongation of the acromion (Fig. 12B). This would be problematic, since, with the exception of the living *Brachycephalus* (Trueb 1973: fig. 2-9a), the procoracoid remains cartilaginous in frogs and tends to disappear in more derived taxa. Furthermore, the supracoracoid foramen of the apparent anterior element (Fig. 12B) would be at some distance from the sup-

posed glenoid (situated above the gap by this interpretation), in contrast to its usual close proximity to the joint. In addition, the foramen would be only partly, if at all, included within the large scaphoid fenestra. Figs. 13C and 14C provide tentative reconstruction of the pectoral girdle of *Triadobatrachus,* based on reexamination (Figs. 13A, 14A) of the holotype material by one of us (SEE), and using the girdle of *Czatkobatrachus* as a model.

We suggest that the displacement that caused separation of vertebral centra IV and V (Rage and Roček 1989: fig. 2B) passed through the weakest parts of the girdle—the glenoid and the foramina. This damage resulted from compression, forcing the robust, dorsally positioned third and fourth ribs down into the more ventral structures. In our opinion, the glenoid should lie within the region of the gap on both sides (denoted by X in Figs. 12 to 14). The structure of the right anterior part of the *Triadobatrachus* specimen is quite similar to the vertically broken specimen Ab.IV/ 28 of *Czatkobatrachus* (Fig. 1B), with its fragment of a glenoid border, and a supraglenoid incision, as well as to the specimen Ab.IV/26 with a supracoracoid foramen in ventral position (Fig. 1A, C). These structures denote the anterior border of the laterally facing glenoid in *Czatkobatrachus*. Hence, we suggest a similar lateral position of the glenoid in *Triadobatrachus*. On the right side, an experimental closure of the gap between the vertebrae (by cutting and pasting parts of original camera-lucida drawings) brings the fragmentary margins of the glenoid closer together. However, the posterior fragment should probably be moved more anteroventral than this to outline a circular, laterally facing glenoid. Then, its originally posterior part (Fig. 13A, B) becomes ventral (Fig. 13C). The shelf-like posterior margin of the scapula region and the arched, anteriorly concave, margin of the coracoid part may be interpreted as parts of the glenoid margin (Fig. 13A). The realignment of the position of the posterior fragment yields a general scapulocoracoid outline that is comparable to that of *Czatkobatrachus* (Fig. 13C). There is no separate coracoid. The apparent posterior elongation of the coracoid part on both sides (Figs. 13A, 14A) is mainly an artifact of preservation.

On the left side, the ventral margin of the glenoid is visible below the humeral head (Fig.14A). The scapular shaft is crossed by the overlying bone elements. A notch apparently corresponding in position to the supracoracoid foramen is visible anteriorly, but the region of a possible supraglenoid cleft is obscured. We suggest that the posterior part of the scapulocoracoid could have been turned around its parasagittal axis in clockwise direction (as seen in a posterior view) during the *post mortem* deformation process, so that a fragment of what is probably the posteroventral or ventral border of the glenoid moved dorsally, and the ventral surface of the coracoid became exposed laterally. The opposite shift is necessary to complete the laterally facing glenoid in our reconstruction (Fig. 14B, C). Its borders are much more damaged than those of the right side, only the supracoracoid foramen being preserved anteroventral to the glenoid.
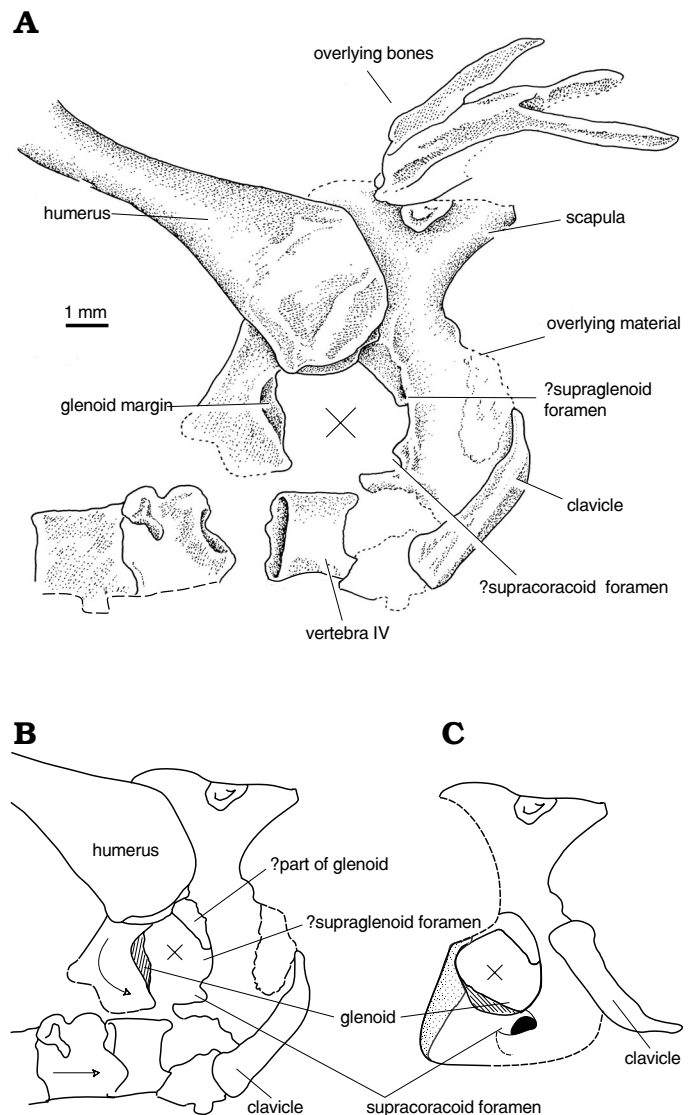

Fig. 13. *Triadobatrachus massinoti* (Early Triassic) right scapulocoracoid in lateral view. **A**. Original drawings by SEE from high fidelity cast of the type specimen MNHN No MAE 126. **B**. Reconstruction scheme. The arrows indicate the proposed shifts of bone fragments. **C**. Right scapulocoracoid reconstructed according to *Czatkobatrachus* pattern with the ventral gap (denoted by X) interpreted as a destroyed glenoid region. The clavicle turned clock-wise to put the wider end proximally as in Rage and Roček (1989: fig. 2B).

The scapular shaft of *Triadobatrachus* is shorter than that of *Czatkobatrachus*, and the distal end of scapula is more expanded. Moreover, the broad distal end protrudes in both directions, with the anterior protrusion making the anterior scapular border concave in contrast to the nearly straight or obliquely oriented margin of *Czatkobatrachus* and primitive tetrapods (see p. 83). In this regard, *Triadobatrachus* is more reminiscent of the basal frogs *Prosalirus*, *Notobatrachus*, and *Vieraella* (Baez and Basso 1996) than of *Czatkobatrachus*.

We suggest that an undivided scapulocoracoid with a relatively elongated scapular blade, a large, rounded, and
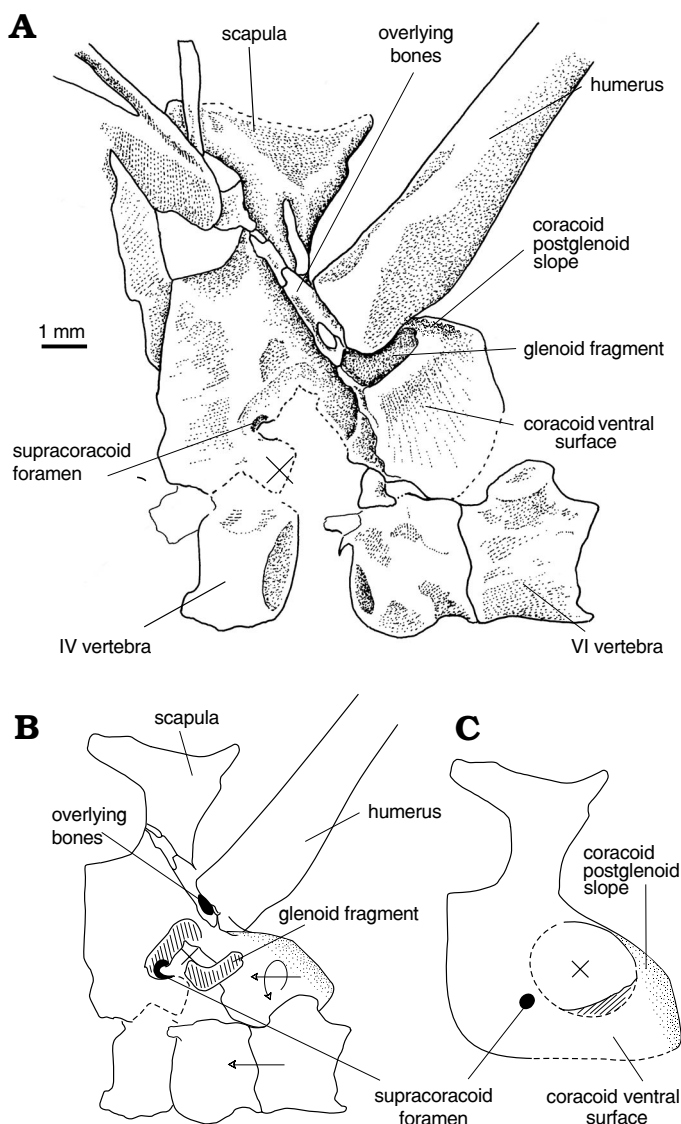
Fig. 14. *Triadobatrachus massinoti* (Early Triassic) left scapulocoracoid in lateral view. **A**. Original drawings by SEE from high fidelity cast of the type specimen MNHN MAE 126. **B**. Reconstruction scheme. The arrows indicate the proposed shifts of bone fragments. **C**. Left scapulocoracoid reconstructed according to *Czatkobatrachus* pattern with the ventral gap (denoted by X) interpreted as a destroyed glenoid region. The clavicle turned clock-wise to put the wider end proximally as in Rage and Roček (1989: fig. 2B).

laterally placed glenoid and a supraglenoid foramen rather than a scapular cleft, is most likely the primitive salientian state for the endochondral pectoral girdle. This leaves a considerable morphological hiatus between the basal condition and that represented by *Notobatrachus* and *Prosalirus*. The Middle Jurassic *Vieraella*, which is the sister taxon of *Notobatrachus* + all crown-group anurans (Baez and Basso 1996), could represent a key intermediate stage spanning this hiatus. Unfortunately, this genus is represented by a single impression in which many details of the scapulocoracoid structure are equivocal (Baez and Basso 1996). Although nothing is known of the structure or position of the glenoid, nor of the pectoral foramina, some as-

pects of the girdle do appear intermediate in *Vieraella*. As illustrated by Baez and Basso (1996: figs. 6, 7), *Vieraella* possessed a fairly slender scapula expanded slightly at its distal end and developing proximally into a subcircular plate (acromial part according to Baez and Basso). Unlike basal taxa, a separate true coracoid was apparently present (Fig. 9B). It appears transversally expanded, although less so than in *Notobatrachus degiustoi*, and is anteroposteriorly shortened, but without developing the narrow proximal peduncle of the younger genus.

Functional remarks

While the new scapulocoracoid material described here cannot definitively solve questions concerning the circumstances (selective pressures) under which salientian locomotion arose, nor permit detailed reconstruction of the pre-anuran stages of its evolution, the new data does contribute to the long-standing discussion on this problem (Gans and Parsons 1966 and references therein). According to Rage and Roček (1989) and Roček and Rage (2000), the appearence of the anuran type skull rather than the anuran type locomotory apparatus was a leading stimulus in the earliest salientian evolution. According to the above authors, modification of the skull may have occured as part of a strengthening of the longitudinal axis as whole, with enlarged cervical muscles providing a firm and almost immobile connection of the head with the trunk. The decrease in number of cervical somites (Richardson et al. 1998) may be an associated phenomenon. Gans and Parsons (1966) considered the anterior elongation of the ilium not primarily a saltatorial adaptation but rather a response to the shortening of the trunk and the consequent requirement to maintain a minimum distance between limbs. So, there is some consensus about the leading role of the body axis in salientian evolution. The shortening of the axis would have acted as a factor making the undulatory movements of the body less effective. The terrestrial mode of life is suggested by numerous osteological features of *Czatkobatrachus*: a high degree of ossification of the elbow joint (Evans and Borsuk-Białynicka 1998), a circular, laterally facing glenoid, and a long narrow scapular blade. Our conclusions with respect to the importance of the forelimbs in supporting the body at the pre-frog stage closely correspond to Gans and Parsons (1966: 95) scenario of a transition from the alternating to a synchronized movements of limbs. According to these authors the animal might have fed with the front of the trunk supported by forelimbs. From this position, it could have used the hindlimbs to push towards the prey while the feet remained in stationary contact with the ground. This movement permitted a gradual development of synchronization. The widely extended forelimb position that we suggest for *Czatkobatrachus* could have helped to maintain balance (preventing the animal falling forward due to the heavy head) at this early phase when the thrust from the hindlimbs was not yet coordinated into an effective jump. However, this construction, and the activation pattern of the neurons involved

at this stage, were probably sufficient for hopping movements. The riparian lifestyle suggested by Gans and Parsons (1966) seems plausible, but any meaningful discussion of this question is beyond the scope of the present paper.

Conclusions

The pectoral girdle of *Czatkobatrachus* permits a clearer comparison between the pectoral structure of basal tetrapods and the highly derived pectoral girdle of crown-group anurans. *Czatkobatrachus* appears to represent an intermediate condition. On this basis, the supraglenoid foramen of basal tetrapods is considered homologous to the anuran scapular cleft, and the cleft scapula is synapomorphic for the Anura. In *Czatkobatrachus*, the subvertical furrow directed from the supraglenoid down to the supracoracoid foramen follows the border between the posterior glenoid buttress, and the anterior scapular part equivalent to the acromion or procoracoid. The width and orientation of the buttress should be directly related to the position of the glenoid and forelimb, and thus to the stresses produced at the shoulder joint. Expansion or reduction of the buttress will directly effect the position of the supraglenoid foramen. The anterolateral shift of the supraglenoid foramen (e.g., that of *Czatkobatrachus*) may have been associated primarily with changes in limb position. The subsequent transformation of the supraglenoid foramen into an anuran type cleft may have been prompted by the requirements of the developing shock-absorption mechanism, in which the coracoid and procoracoid/clavicle diverged in the direction of the axis of the ventral side of the body, thus leaving a neutral (unstressed) section between their scapular articulations. This, and the general shortening of the body axis, may have been accompanied by changes in the structure and relations of the brachial nerves and blood vessels (their posterior translation).

Given that *Czatkobatrachus* and *Triadobatrachus* represent a similar stage of salientian evolution, the scapulocoracoid of the latter genus may be interpreted as a single plate with a laterally facing glenoid. The two genera differ principally in the shape of the scapular blade, confirming their generic distinction.

For the lightly built but well-ossified *Czatkobatrachus*, a predominantly terrestrial lifestyle seems most plausible, but this may not have been the case for *Triadobatrachus* (Rage and Roček 1989). Here we have interpreted the laterally rotated but dorsoventrally extended glenoid as permitting the body to be carried well above the substrate. This suggests terrestrial walking, with a possibility of hopping movements, possibly in an essentially riparian environment (as suggested by Gans and Parsons 1966). The feeding strategy proposed by these authors with the body supported by forelegs and aided by hindlimb thrusts, is here considered plausible, as is the hypothesis that this stage provided motor-unit training for symmetrical activation. Perhaps the more elevated body position also aided buccal pump breathing, while the ability to hop suddenly into water may have been a useful defense mechanism (Gans and Parsons 1965). In this context, the proposed aquatic lifestyle of *Triadobatrachus* may be secondarily derived from the terrestrial pre-frog pattern.

Acknowledgments

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