

# Certain Features of the Postcranial Skeleton of *Vivaxosaurus permirus* Kalandadze et Kurkin (Anomodontia, Dicynodontidae), with a Note on Their Presumable Trophic Adaptation

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**Abstract**—Postcranial bones of *Vivaxosaurus permirus* Kalandadze et Kurkin are described. Certain features of the pectoral girdle and forelimbs suggest adaptation to feeding on subterranean plant organs. Structural features of the acetabulum of *Vivaxosaurus* are indicative of its close relationship to Triassic anomodonts.

**Key words:** *Vivaxosaurus*, Dicynodontidae, Upper Permian, postcranial skeleton, trophic adaptations.

## INTRODUCTION

Reconstruction of adaptations of extinct tetrapods is a fascinating field of paleontology. In this respect, anomodonts are a very promising and poorly understood therapsid group. In the Late Permian and Triassic, various anomodont groups dominated herbivore communities and undoubtedly adapted to feeding on plants from various vegetable stories in various environmental conditions. Occasionally, this group gave rise to unusual forms, such as Early Triassic *Lystrorhynchus* (Watson, 1912, 1913), which was most likely adapted to a semiaquatic mode of life, and even subterranean Late Permian *Cistecephalus* and *Kawingosaurus* (Cox, 1972; Cluver, 1978). Morphological adaptations of other taxa manifest themselves to a much lesser extent; therefore, they are difficult to recognize and interpret with certainty, especially in the case of poorly preserved fossil specimens. Nevertheless, even fragmentary material sometimes provides informative data for the reconstruction of certain features of the animal's lifestyle. Such is the case with the postcranial specimens of the Late Permian dicynodont *Vivaxosaurus* (Kalandadze and Kurkin, 2000); specific characters of this animal enable one to reconstruct certain features of its mode of life.

The specimens examined in the present study are stored at the following institutions: (BMNH) British Museum of Natural History, London; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; and (UT) Universität Tübingen Museum und Institut für Geologie und Paläontologie, Tübingen.

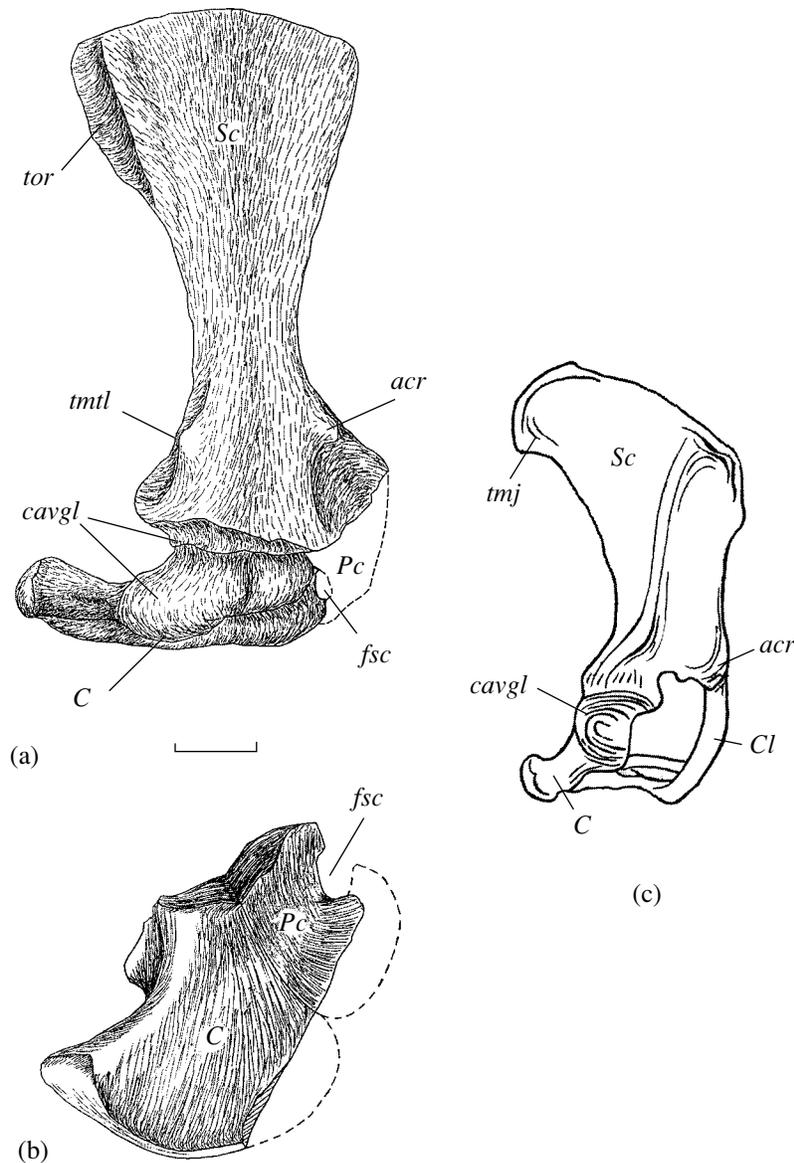
## DESCRIPTION

The postcranial skeleton of *Vivaxosaurus permirus* Kalandadze et Kurkin 2000 (holotype PIN, no. 1536/1;

Upper Permian, Vyatkian Horizon; Berezhane locality, Kirov Region) is represented by isolated complete bones and numerous fragmentary remains. The right and left coracoid plates represented by fused coracoids and procoracoids, a complete left humerus, the proximal region of the right humerus, a complete right scapula, and the distal region of the left scapula are relatively well preserved and allow for identification.

**Scapula** (Fig. 1a, Sc). The complete right scapula is 280 mm long (along the midline). The blade markedly expands dorsally. The upper margin is convex and 185 mm wide; judging from its slightly tuberculate surface, it was covered by cartilage during the animal's life. The lateral surface of the scapula is weakly concave. The upper third of the posterior margin is provided with a broad ridge (torus) extending along the lateral surface; posteriorly, it considerably expands and slightly curves inside. The lower end of the bone is stout and 120 mm wide. The acromion (Fig. 1a, *acr*) occupies a low position only 40 mm above the glenoid fossa. At the level of the acromion, the posterolateral edge of the bone has a small tubercle for the long head of the triceps (Fig. 1a; *tmtl*). The glenoid fossa (Fig. 1a; *cavgl*) is irregular in shape (80 × 60 mm) and ventrolaterally oriented.

**Coracoid and procoracoid.** The coracoids and procoracoids of *Vivaxosaurus* are fused to form an integrated plate (Fig. 1b). The coracoid (Fig. 1b, C) is a stout bone; its posterior edge is concave, while the medial edge is rounded and substantially posteriorly thickened. The posterior margin is massive, an approximately 30-mm-long groove passes along its midline. Laterally, the bone is extremely stout in the region of the glenoid fossa; its articular surface is divided into two unequal parts. The smaller facet is triangular, 40 ×



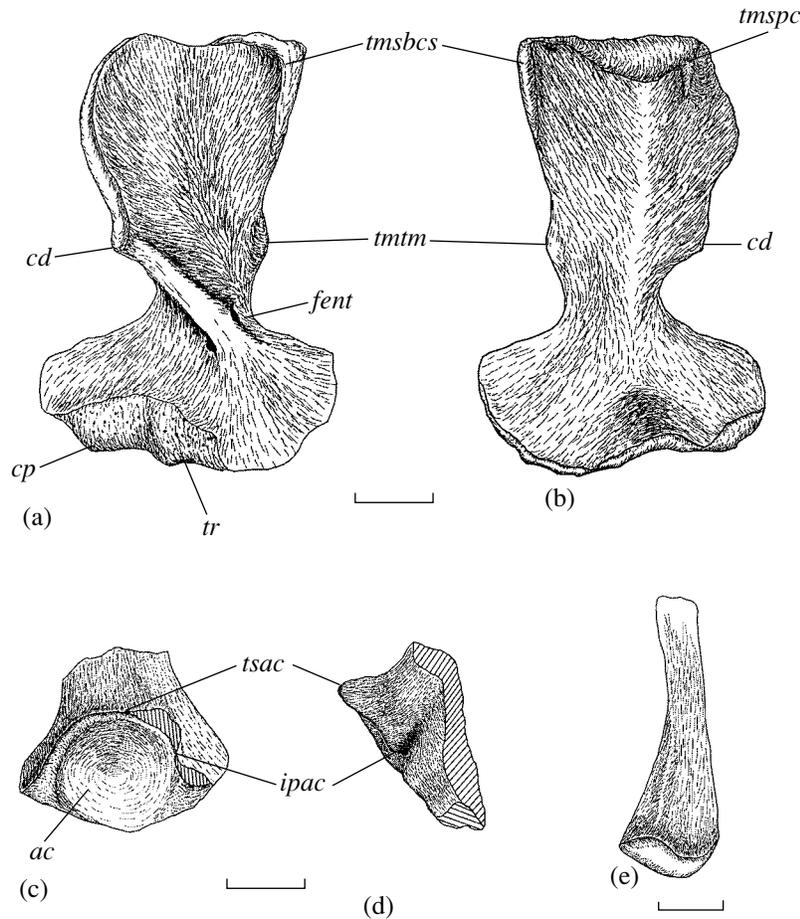
**Fig. 1.** Pectoral girdles of (a, b) *Vivaxosaurus permirus* Kalandadze et Kurkin (holotype PIN, no. 1536/1): (a) lateral and (b) ventral views; and (c) *Echidna* (schematic, after Westling, 1889). Designations: (C) coracoideum, (Cl) clavicle, (Pc) procoracoideum, (Sc) scapula, (acr) acromion, (fsc) supracoracoid foramen, (cavgl) glenoid cavity, (tmj) teres major muscle, (tmtl) tubercle for the triceps, and (tor) torus (ridge). Scale bar, 40 mm.

30 mm in size, and articulated with the scapula. The glenoid area of the articular surface is somewhat larger ( $45 \times 35$  mm), irregular in shape, and longitudinally extended.

The procoracoids (Fig. 1b; *Pc*) are irregular in shape. The anteromedial edge of each bone is damaged. The lateral margin of the bone is massive, triangular in section,  $40 \times 45$  mm in size; its surface is convex and divided into two almost equal parts for the glenoid fossa and for the articulation with the scapula. An ovoid 25-mm-deep and 10-mm-wide incisure for the supracoracoid foramen is located anterior to the scapular facet (Fig. 1b, *fsc*). This foramen is almost completely closed

by the procoracoids, except for the lateral border, which is formed by the scapula.

**Humerus** (Fig. 2). A complete humerus is 216 mm long. Its proximal epiphysis is stout and pulley-shaped in cross section. The articular surface is convex and covered by large tubercles; during the animal's life, it was covered by thick cartilage. In the posterodorsal region of the bone, the proximal epiphysis has a stout and extended 75-mm-long ridge covered by fine undulating ornamentation (Fig. 2, *tmsbcs*). Distal to this ridge, the bone has a small ovoid tubercle for the medial head of the triceps (Fig. 2, *tmtm*). The anteroventral surface of the bone has a 55-mm-long ridgelike projection



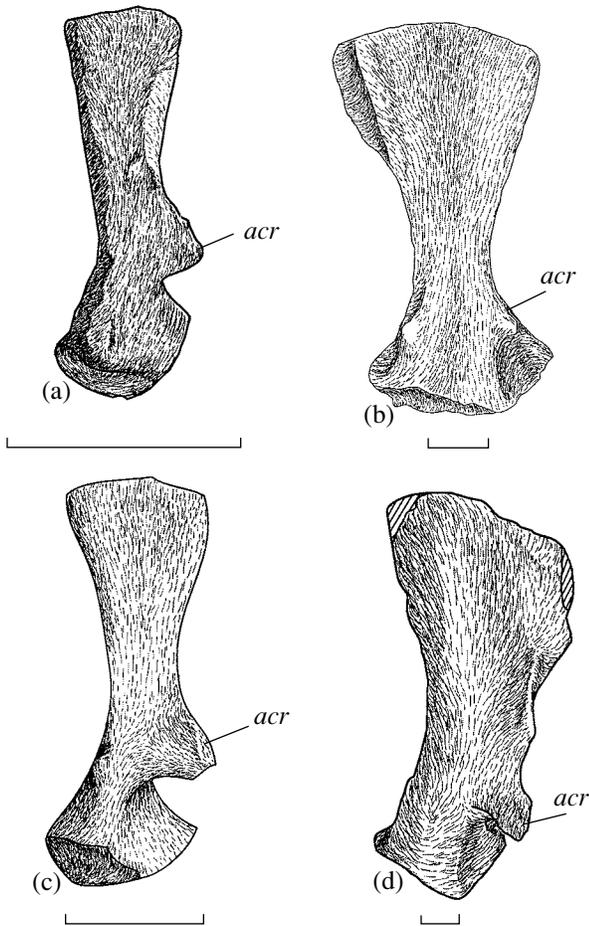
**Fig. 2.** Limb bones and pelvic fragments of *Vivaxosaurus permirus* Kalandadze et Kurkin (holotype PIN, no. 1536/1): (a, b) right humerus, posteroventral and anterodorsal views; (c, d) acetabular region of the left ilium, external and rear views; and (e) distal part the left fibula. Designations: (*ac*) acetabulum, (*cd*) crista deltopectoralis, (*cp*) capitulum, (*fent*) foramen entepicondylar, (*ipac*) incisura postacetabulum, (*tmtm*) tubercle for the triceps medialis muscle, (*tmsbcs*) torus for the subcoracoscapularis muscle, (*tmspc*) torus for the supracoracoidalis muscle, (*tr*) trochlea, and (*tsac*) tuber supracetabularis. Scale bar, 40 mm.

near the proximal epiphysis (Fig. 2, *tmspc*); this ridge was most likely the attachment area for the supracoracoid muscle. The deltopectoral crest (Fig. 2, *cd*) is broad, massive, and extends distally for two-thirds of the bone length. On the ventromedial side, it becomes a massive ridge for attachment of the humeral biceps; this ridge is pierced by a large entepicondylar foramen (Fig. 2a; *fent*). The distal epicondyles are broad (the distal epiphysis is 163 mm wide); the entepicondyle is more massive than the ectepicondyle. The articular surfaces for the radius (Fig. 2a, *cp*) and ulna (Fig. 2a; *tr*) are convex and covered by small pits; the ulnar condyle is smaller than that for the radius.

**Ilium** (Figs. 2c, 2d). The collection contains a proximal fragment of the ilium, including the acetabulum. The bone is massive; above the acetabulum, it is 55 mm wide; ventrally, it expands and becomes 110 mm wide at the level of the lower third of the acetabulum. The supra-acetabular crest is stout and very broad (Figs. 2c, 2d; *tsac*). It forms a 25-mm-high and 75-mm-wide pro-

jection that borders the acetabulum dorsally and partially posteriorly. The postacetabular incisure is relatively shallow (Figs. 2c, 2d, *ipac*). The acetabulum is slightly ovoid, spherically concave, and 65 mm in diameter (Fig. 3c; *ac*). The articular facets for the pubis and ischium face ventrally. The pubis is larger than the ischium; it is irregular trapezoid in shape, 60 mm long, and 40 mm wide. The articular facet for the ischium is longer and narrower (70 × 20 mm) than that for the pubis. The facets for the ischium and pubis are positioned at an angle of about 120° to each other.

**Fibula** (Fig. 2e). Only the distal region (about 160 mm long) of the left fibula is preserved. The bone is narrow, its diaphysis is 25 mm in diameter. The distal epiphysis is substantially widened and slightly ovoid in cross section. The articular surface is slightly convex and gently narrows posteriorly. The transverse and longitudinal diameters of the epiphysis are 40 and 45 mm, respectively.



**Fig. 3.** The position of the acromion relative to the glenoid fossa in dicynodonts of different size; (a) *Pelanomodon halli* (specimen BMNH, no. R4067); (b) *Vivaxosaurus permirus* (specimen PIN, no. 1536/1); (c) *Rhinodicynodon gracile* (specimen PIN 1579/50); and (d) *Stahleckeria potens* (specimen UT, no. n1). For designations, see Fig. 1. Scale bar, 40 mm.

## DISCUSSION

Although the postcranial specimens described above are rather fragmentary, they display a number of characteristics that allow for a tentative reconstruction of the mode of life of *Vivaxosaurus permirus* and discovery of certain features of the general structural pattern of the postcranial skeleton in anomodonts.

The substantially posteriorly widened blade of the scapula equipped with the longitudinal ridge on the lateral side (Fig. 1a, *tor*) is a characteristic morphological feature of the postcranial skeleton of *Vivaxosaurus*. This area undoubtedly provided the attachment for strong muscles, which are reconstructed on the basis of comparative analysis of living reptiles and mammals (Fürbringer, 1900; Romer, 1922; Gurtovoi and Dzerzhinsky, 1992). The major muscles originating from the caudal part of the reptile scapula are the subcoracoscapular muscle, which is attached on the inner

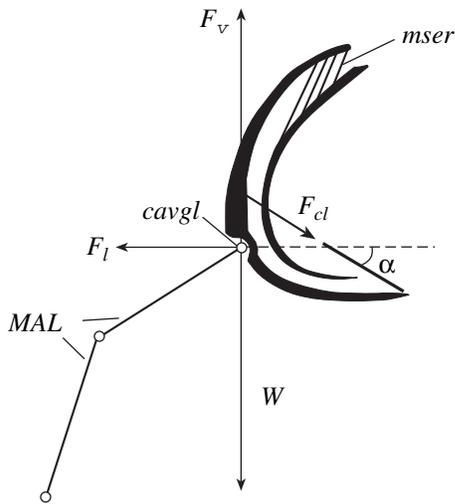
side along the posterior edge of this bone, and the serrate muscles, which connect the dorsal side of the scapula with the trunk. Mammals have acquired an additional muscle (the teres major muscle), which also originates from the posterior corner of the scapula.

The strongly posteriorly extended upper corner of the scapula of *Vivaxosaurus* undoubtedly reflects its specialization and strengthening of the musculature originating from this area. It is highly improbable that the area under study is associated with the attachment of the posteriorly displaced and strengthened serrate musculature, since the displacement of these muscles onto the posterior corner of the scapula is usually associated with the development of parasagittally oriented limbs, as is observed in mammals (Kuznetsov, 1999).

The original structure of the scapula in *Vivaxosaurus* is most likely associated with the dorsal position of the strengthened subcoracoscapular musculature, which originates from the same region of the inner surface of the scapula in living reptiles and mammals (Romer, 1922; Gurtovoi and Dzerzhinsky, 1992). One may interpret the broad ridgelike expansion along the dorsal margin of the scapula (Fig. 1a, *tor*) as the attachment area for the teres major muscle. Unfortunately, it is impossible to conclude this with certainty, since the ridge on the posterodorsal surface of the humerus (Fig. 2a, *tmbscs*), which is located in the area of probable attachment of the teres major and subcoracoscapular muscles, is not divided into two.

The unusually strong subcoracoscapular muscles and probably well-developed teres major muscles of *Vivaxosaurus* undoubtedly participated in the strong and prolonged posterior and lateral movement of the humerus combined with its rotation in the glenoid fossa. Among extant animals, a similar specialization of the scapulocoracoid (where the posterior corner of the scapula is posteriorly extended and the retractors of the humerus are well developed) is observed in echidnas (Fig. 1c) (Westling, 1889), which regularly use their forelimbs for digging. The similar structural pattern of the pectoral girdle in echidna and *Vivaxosaurus* suggests that the forelimbs of the latter were also adapted for digging, in particular, for the extraction of subterranean plant organs. These data agree with such cranial characters as the strongly inclined occiput, a bend in the palatal surface, and stout and vertically positioned canines, which were proposed to be an adaptation “for digging out subterranean parts of plants, undermining their root system, or destruction of large vegetative elements” (Kalandadze and Kurkin, 2000, p. 66)

In the context of the above concept of trophic adaptations of *Vivaxosaurus*, of special interest are the data obtained by Arefiev and Naugolnykh (1998) in the course of reconstruction of the Late Permian catena. The researchers recognized three sedimentation regions located at different distances from a basin and characterized by different types of root systems. The zone located close to the basin (periodically flooded



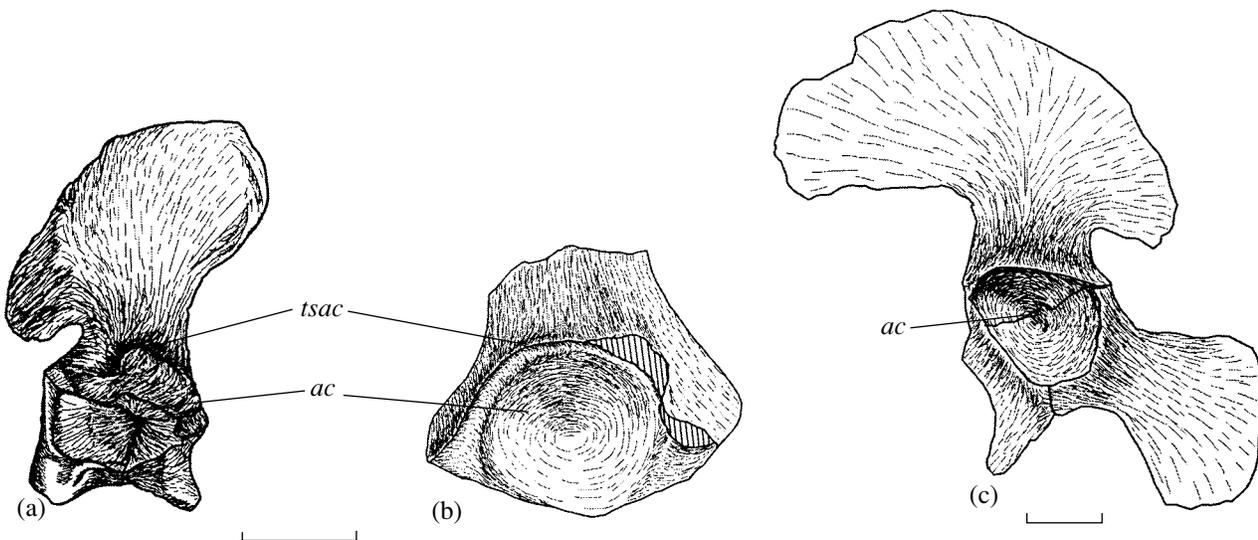
**Fig. 4.** Schematic cross section of the therapsid pectoral girdle (after Jenkins, 1971, modified) and its mechanics in a static position. Designations: (*cavgl*) glenoid cavity, ( $F_{cl}$ ) counterforce to the lateral displacement of the scapulocoracoid, ( $F_l$ ) lateral component of the supporting force, ( $F_v$ ) vertical component of the supporting force, (*mser*) serrate muscles, (*MAL*) mechanical limb axis, ( $W$ ) body weight, and ( $\alpha$ ) angle between the clavicle and the horizontal.

area of the nearshore lowland) is characterized by ephemeroids with a thick and shallowly penetrating root system. Farther from the basin, in the subaerial region of intense soil formation, they were replaced by plants similar to ephemeroids and characterized by abundantly branching roots. The third zone was even farther from the basin where sedimentation was produced by floods (playa); it was occupied by phreato-

phytes, whose root systems were composed of stout, vertically extended, and only slightly branching roots, which occasionally had ovoid bodies (probably, formed of reserve matter). It is highly plausible that such phreatophyte roots with expansions rich in storage matter could be an important component in the diet of *Vivaxosaurus*, which probably inhabited these areas.

Another characteristic feature of the pectoral girdle of *Vivaxosaurus* is the low position of the acromion. Comparative analysis of the pectoral girdle in Permian and Triassic dicynodonts displayed a positive correlation between this character and the individual size (Fig. 3). This character is attributable to the general structural pattern of the pectoral girdle of dicynodonts, which is characterized by widely spaced limbs. This feature is typical of all primitive therapsids and causes the medial inclination of the scapula and appropriate position of the serrate muscle (Jenkins, 1971). Since the above mentioned muscles played the major role in the attachment of the scapulocoracoid to the trunk, in the case of the medially curving scapula, the projection of the attachment area of these muscles on the horizontal plane fell beyond the glenoid fossa; this produced a force that displaced the proximal end of the scapula laterally (Fig. 4). This force ( $F_l$ ) was directed horizontally and changed proportional to the animal's weight. The clavicles compensated this force and prevented the dislocation of the scapula by the force  $F_{cl}$ , which was proportional to the cosine of the angle between the clavicle and the vector  $F_l$ :

$$F_{cl} = \frac{F_l}{\cos \alpha}.$$



**Fig. 5.** Pelvic girdles of dicynodonts: (a) *Pelanomodon halli* (specimen BMNH, no. R4067); Upper Permian, *Dicynodon* Zone; South Africa; (b) acetabulum of *Vivaxosaurus permirus* (specimen PIN, no. 1536/1); Upper Permian, Vyatkian Horizon; Russia; and (c) *Shansiodon* sp. (specimen BMNH, no. R12 710); Middle Triassic, Manda Formation; Tanzania. For designations, see Fig. 2. Scale bar, 40 mm.

According to this equation, the compensatory force preventing the lateral dislocation of the scapula grows with  $\cos\alpha$  and reaches its maximum when the angle  $\alpha$  tends to zero, that is, the acromion is in the extreme low position.

In addition to the above functional morphological features of the pectoral girdle, certain other evolutionary advanced characters of *Vivaxosaurus permirus* are worthy of notice. This concerns certain characters distinguishing *Vivaxosaurus* from advanced Late Permian dicynodontids (i.e., the taxa characterized by the reduced tooth row), such as the more rounded and lateroventrally oriented acetabulum, which also differs in the extremely broad supra-acetabular projection combined with a small, almost completely reduced, postacetabular incisure. Such an acetabulum is more similar to that of Middle Triassic taxa (Fig. 5) whose pelvic girdle provided a more parasagittal position of the hind limb (Surkov, 1998).

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