

Morphofunctional analysis of the cervical-thoracic region in some burrowing mammals

Petr P. Gambaryan, Olga V. Zhrebtsova & Vladimir V. Platonov

ABSTRACT. The comparative analysis of such high specialized burrowers as *Talpa europaea*, *Spalax microphthalmus*, *Nannospalax nehringi*, *Myospalax myospalax* and generalized non-burrowing *Rattus norvegicus* was carried out to reveal their adaptive peculiarities in the skeleton and muscles structure of cervical-thoracic region. In *Talpa* during the pushing the soil apart with the forelimbs the drawing of head backwards between the hands is observed. It results in arched neck position, atlas being displaced on the ventral parts of the occipital condyles. At the drawing the head forward during the searching of food the role of *m. longus colli* is most important. For its insertion in *Talpa*, in contrast to that of other burrowers and *Rattus*, the specific ventral plates are developed not only on the sixth, but also on the fourth and fifth cervical vertebrae. The particular mobility in thoracic region in *Talpa* testifies that during the throwing out the soil the forelimbs are used. *Spalax*, *Nannospalax*, and *Myospalax*, on the contrary, throw the soil out with the head. It becomes possible at the significant consolidation of the cervical vertebrae by the sharp decreasing of their mobility up to the partial accretion. However, in comparison to *Rattus* and *Talpa*, the higher mobility in the occipital joint is observed. Moreover, the increasing of solidity of the first thorax segment and formation of the specific withers on the second–sixths (seventh) thoracic vertebrae take place. Three main groups of the muscles (extensors of occipital and elbow joints; the muscles lifting the body between the forelimbs) acting at the process of throwing the soil with the head in spalacids and *Myospalax* are about four–six times stronger than such in *Rattus*; the extensors of the occipital joint are 20 times stronger than those in *Talpa*.

KEY WORDS: Talpidae, Spalacidae, Myospalacidae, skeleton, musculature, burrowing.

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Морфофункциональный анализ шейно-грудной области у некоторых роющих млекопитающих

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РЕЗЮМЕ. Для выявления адаптивных особенностей в строении скелета и мышц шейно-грудной области было проведено сравнение таких специализированных землероев как кроты (*Talpa europaea*), слепыши (*Spalax microphthalmus*, *Nannospalax nehringi*) и цокоры (*Myospalax myospalax*) с универсальной, нероющей формой (*Rattus norvegicus*). У крота при раздвигании грунта лапами происходит оттягивание головы назад между конечностями. Это приводит к дугообразной постановке шеи, при этом атлант занимает вентральную часть затылочных мыщелков. При вытягивании шеи вперед во время поиска корма основную роль играет *m. longus colli*, для прикрепления которой у *Talpa*, в отличие от других изученных форм, не только на шестом, но и на четвертом-пятом шейных позвонках развиваются специальные вентральные пластинки. Развитие особой подвижности в грудной области свидетельствует в пользу того, что и при выкидывании земли кроты пользуются лапами. *Spalax*, *Nannospalax* и *Myospalax* выбрасывают землю на поверхность головой. Это становится возможным при жесткой консолидации шейных позвонков путем резкого уменьшения их подвижности, вплоть до срастания ряда из них. Однако по сравнению с *Rattus* и *Talpa* более высокая степень подвижности наблюдается в области затылочного сустава. Отмечается также повышение жесткости первого сегмента груди и развитие специальной холки на втором–шестом (седьмом) грудных позвонках. Три основные группы мышц (разгибатели затылочного и локтевого суставов; мышцы, поднимающие туловище между конечностями), работающие при выталкивании земли головой, у спалацид и *Myospalax* в 4–6 раз сильнее, чем таковые у *Rattus*, а разгибатели затылочного сустава у них в 20 раз сильнее, чем у *Talpa*.

КЛЮЧЕВЫЕ СЛОВА: Talpidae, Spalacidae, Myospalacidae, морфология, скелет, мускулатура, рытье.

Introduction

The digging activity of the high specialized subterranean mammals usually consists of the loosening the soil and throwing it outside. The latter can be realized by different ways. The burrowers of Spalacidae, Myospalacidae, Geomyidae and Chrysochloridae throw the earth away with their head (Hill, 1937; Gambaryan, 1960, 1978; Gasc *et al.*, 1986; Gambaryan & Gasc, 1993). There are two opinions on digging technique of the common mole, *Talpa europaea* Linnaeus, 1758. According to one of them the animal throws the soil out with the head and withers (Folitarek, 1932; Formozov, 1952; Stroganov, 1948). Hisaw (1923) described that the North American mole, *Scalopus aquaticus* (Linnaeus, 1758) acts with the forelimbs only. The same was observed in *T. europaea* by using the cinefluorography (Gambaryan *et al.*, 2002). What the morphological alterations of the locomotor organs are involved by an adaptation to the throwing the soil out in the burrowing mammals? To clear the matter up the axial skeleton and musculature of the cervical and thoracic regions principally and the muscles of the forelimbs partly were investigated in some forms of Spalacidae, Myospalacidae, and Talpidae. The comparative morphofunctional analysis served also to clarify the controversial question on digging mode of *T. europaea*. The comparison with such universal, non-burrowing form as Norway rat, *Rattus norvegicus* (Berkenhout, 1769) likewise was made to reveal the adaptive properties of the musculoskeletal system in the high specialized burrowers.

Material and methods

The muscles and skeleton morphology was studied based on specimens from the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg. The adult specimens of common mole, *Talpa europaea* (n=3), Norway rat, *Rattus norvegicus* (n=3), Siberian zokor, *Myospalax myospalax* (Laxmann, 1773) (n=3), common mole-rat, *Spalax microphthalmus* Güldenstaedt, 1770 (n=2), and Nehring's mole-rat, *Nannospalax nehringi* (Satunin, 1898) (n=2), formalin preserved were used for the morphofunctional analysis of the axial cervicothoracic musculature and some muscles of the forelimbs. The morphological peculiarities of the occipital joint, cervical and thoracic vertebrae were investigated also using the greater sets of skeletons (n=4–10). Through the muscles dissection their detailed description and weight analysis were made for all the species listed above. In this connection a total weight of the fore and hind limbs muscles served as basis for a relative weight calculation of the axial muscles.

To analyze the functional characteristics of the locomotor apparatus the cinefluorographic data on the digging activity of *S. microphthalmus* were also used. In this case a graphical method was applied to determine the mechanical effects of the muscles. The length of the force vector was assumed to be proportional to

the theoretical physiological section of muscle (=its mass divided by the average fibre length). For calculation of the latter up to ten fibres of each muscle analyzed were measured. The direction of the force vectors was determined by the muscle topography accurately described. The vectors of synergists were summed. The summary force calculation in the case of *m. serratus ventralis* separate parts may serve an illustration of this graphical method (Fig. 1). One can see the changes of the muscle force and direction in connection with the modifications of skeleton position at the beginning and at the end of the phase of throwing the soil outside with the head in *S. microphthalmus*.

The angles determining the head mobility were measured by application of camera Lucida and are as follows:

1) An angle of the occipital condyle slope (in parasagittal plane of the skull) — at intersection of the palate surface line and perpendicular to the line connecting two points (first in the extreme upper and second in the extreme lower parts) on the condyle basis (Fig. 2A);

2) An angle of the atlas vertical displacement (in parasagittal plane of the skull) — at intersection of two straight lines drawn through the same two arbitrary points on the atlas surface but one line — at the extreme upper and second — at the extreme lower positions of atlas on the occipital condyle (Fig. 2B);

3) The total angle of the atlas lateral displacement (in frontal plane of the occipital joint) — at intersection of the atlas longitudinal axes in its two extreme lateral positions on the occipital condyle surface, the reliable contact of the articular surfaces being still retained (Fig. 2C);

4) The total angle of rotation between the atlas and axis (in frontal plane of the vertebrae) — at intersection of the atlas longitudinal axes in its rotation around axis from one extreme position to another, the reliable contact of the articular surfaces being still retained (Fig. 2D).

For short, we refer hereafter to the species investigated by the generic names only.

Abbreviations. m. — muscle, mm. — muscles, p. — pars, pr. — processus, lig. — ligamentum.

Peculiarities of the cervical vertebral morphology

Occipital joint

Much of the head mobility is dependent on the form and position of the occipital condyles and the cranial articular facets of atlas. The articular surface of the occipital condyle in *Rattus* can be divided into two expended parts (upper and lower) connected by an isthmus of varied width. Craniolaterally to the latter there is a foramen for the XII cranial nerve. The upper part of the articular surface is greater and more convex than its lower part. It widens also rather abruptly (about

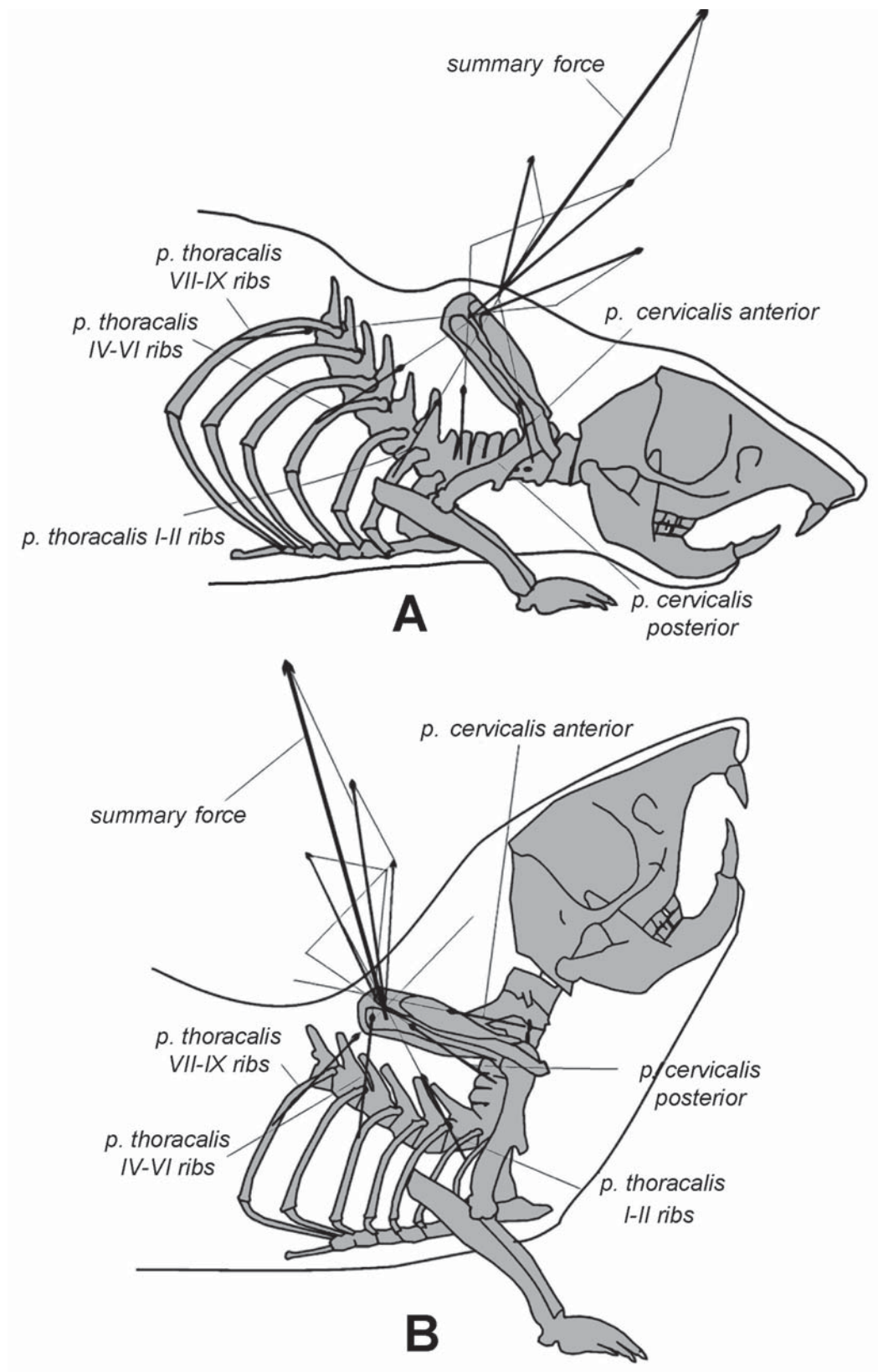


Figure 1. Graphical method of the summary force determination on the example of m. serratus ventralis in *Spalax microphthalmus*. Positions corresponding to the beginning (A) and the end (B) of throwing the soil out.

Abbreviation: p. — pars.

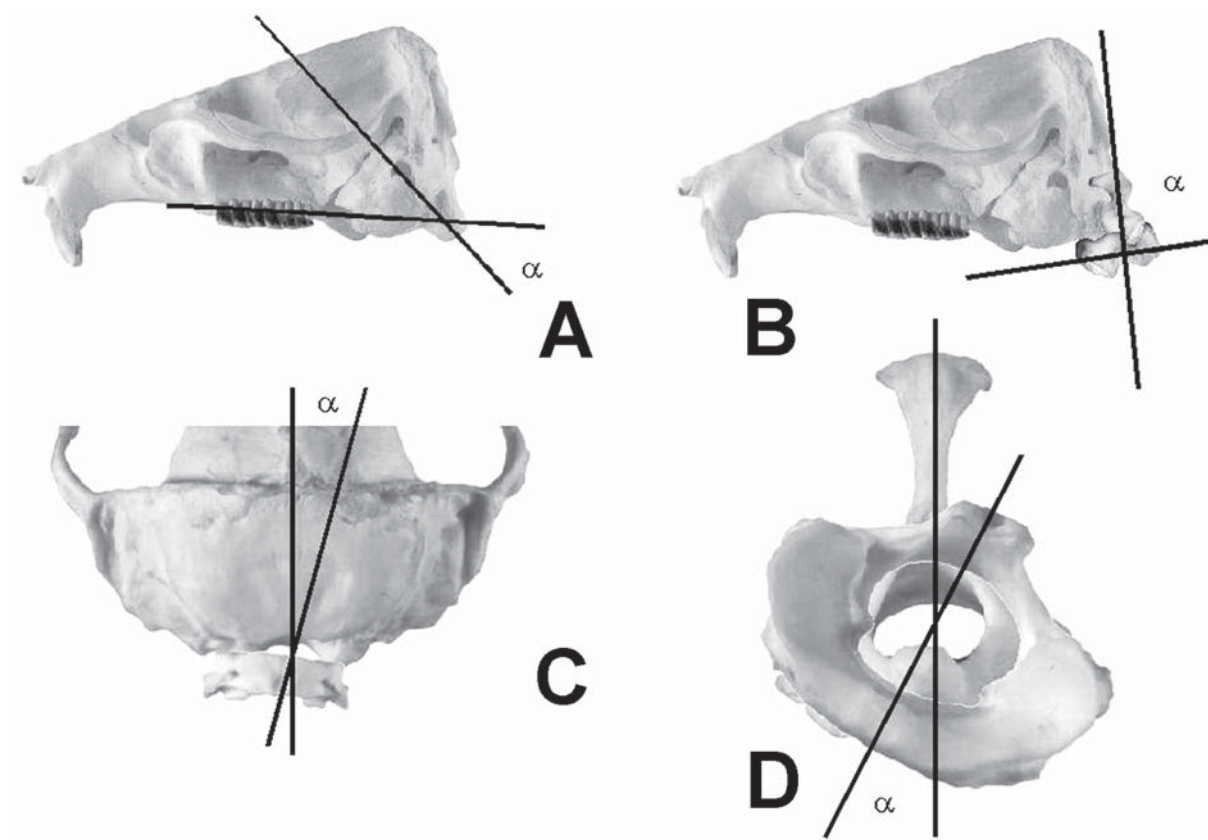


Figure 2. Methods of measurement of the angles providing the head mobility: A — an angle of the occipital condyles slope to the os palatinum plane α ; B — whole angle of atlas vertical displacement in the occipital joint α ; C — half of whole angle of atlas lateral displacement in the occipital joint α ; D — half of whole angle of atlas rotation in the atlas-axis joint α .

2.5–2.8 times) changing gradually in direction from dorsocaudolateral to ventrolateral (Figs. 3–6). The lower part of the condyle articular surface is mainly facing cranioventrally and does not contact with the opposite condyle along the skull midline. A total angle of the occipital condyle slope in *Rattus* is about 40° (Fig. 5A; Tab. 1). The caudal margin of the condyle lower facet does not protrude beyond the margin of the foramen magnum. The form of foramen magnum is close to a symmetrical pentagon with the central top rounded to a different extent. Contrastingly, the margin of the condyle upper facet projects significantly beyond the foramen edge.

In *Spalax* and *Nannospalax* the occipital condyle is strongly convex and its comparatively wide articular surface is without isthmus. The upper part of the latter is facing more dorsally and less laterally in contrast to that of *Rattus*. Its medial margin is turned inside to a greater extent than in rat, and is nearly parallel to the medial margin of the opposite condyle (Fig. 4B). In this instance an angle of the occipital condyle slope is significantly less than that in *Rattus* (Tab. 1). On the ventral side of the skull the condyle articular facet is narrowed and thickened gradually, and contacts with the opposite condyle along the midline (Fig. 3B). In the caudal view the foramen magnum is fungiform (Fig. 4B).

In *Myospalax* the upper articular surface of the occipital condyle has a similar dorsoventral widening (about two times) as in *Rattus*. However, its lateral turn is expressed weakly as in *Spalax*. In contrast to the latter the medial margins of the condyles in *Myospalax* are not parallel in caudal view and deviate laterally in their upper parts but less than in *Rattus* (Fig. 4C). At the same time the dorsal component of the turn of the upper articular surface in *Myospalax* is similar to that in *Rattus*. Thus, an angle of the occipital condyle slope in *Myospalax* is intermediate between those in *Rattus* and *Spalax* (Tab. 1). In contrast to the latter, on the ventral side of the skull the articular facets of condyles in *Myospalax* are not narrowed and do not contact along the midline. The form of the foramen magnum in *Myospalax* is hexagon-like (Fig. 4C).

In *Talpa* occipital condyles project very weakly on the occipital part of the skull framing the margins of the foramen magnum. As a result the radius of their curvature in *Talpa* is greater than in other species mentioned above. The shape of the foramen magnum is close to oval with outlines passing gradually from the caudal part of the skull to the ventral one (Figs. 3D, 4D). In this case, the ventral component of the foramen longitudinal axis is nearly equal to the caudal one, in contrast to the condition in other taxa studied. The occipital part of

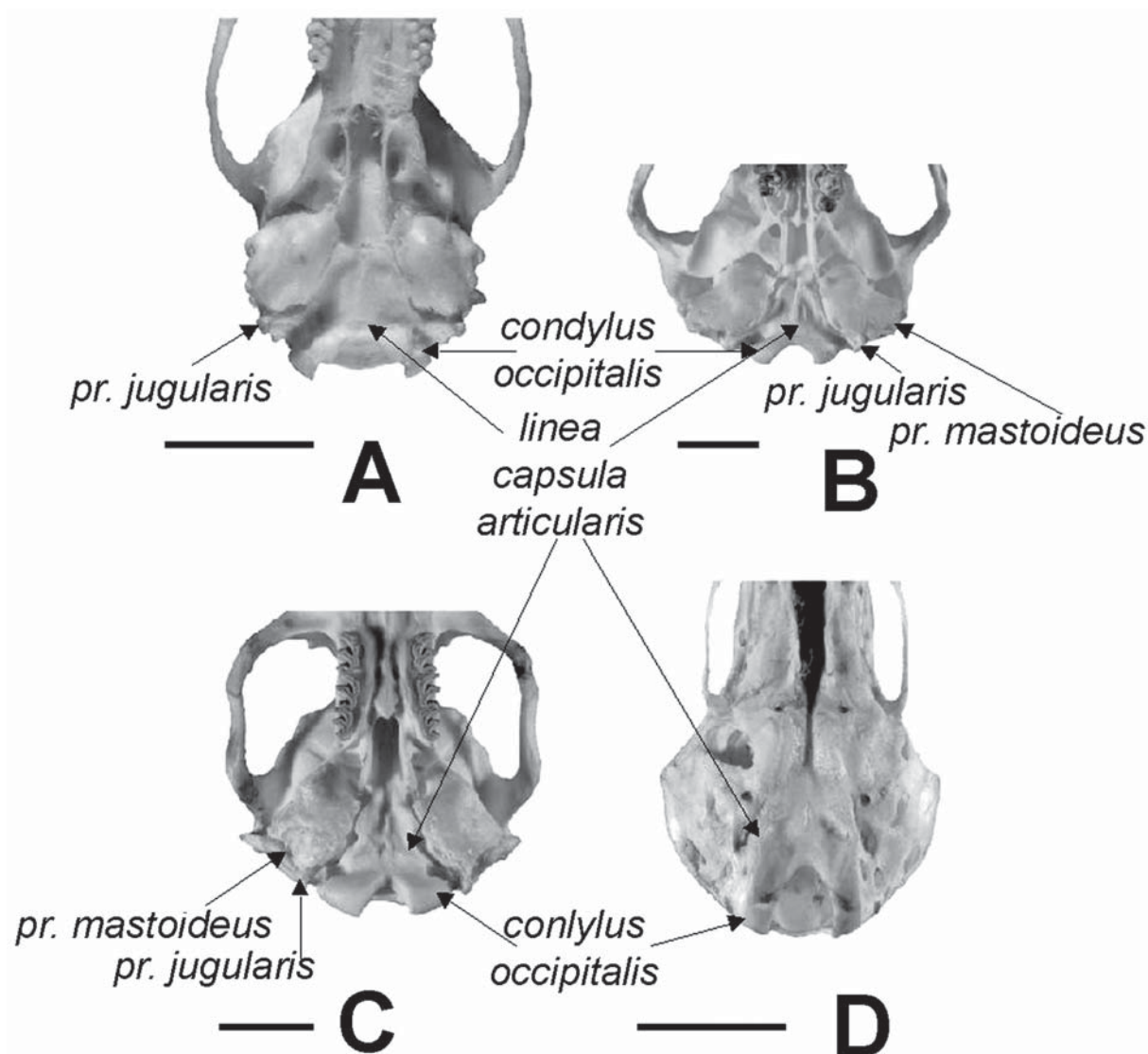


Figure 3. The occipital region of the skull in ventral view.

A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*. Scale bars are 1 cm.

the skull in *Talpa* is smooth and rounded as compared with *Spalax* and *Myospalax*, where it is covered by numerous crests, ridges and irregularities.

The articular surface of the occipital condyle in *Talpa* is subdivided by small medial incisura into two parts (upper and lower), like in *Rattus*. However, in contrast to the latter, the condyle upper part is smaller than the lower part, and directed ventrocaudolaterally rather than ventrocaudodorsally. As a result an angle of the condyle inclination in *Talpa* exceeds that in *Rattus* (Tab. 1). The medial margins of the upper articular parts do not project beyond the margins of the foramen magnum and are parallel to each other (Figs. 3D, 4D). The condyles lower parts retain the cranioventral direction without contact along the skull midline. However, in contrast to those in all taxa mentioned above these condylar parts in *Talpa* extends beyond the margins of

the foramen magnum and are narrowing gradually (Fig. 3D). Thus, the most part of the strongly flattened occipital condyles is placed on the ventral surface of the skull.

The kidney-like form of the cranial articular facet of atlas with the considerable ventral narrowing in *Rattus* reflects the shape of the occipital condyles (Fig. 7A). At the same time, the dorsal narrowing region, which is characteristic of the latter, is lacking on the atlas cranial articular facet. Its surface in *Rattus* does not extend above a level of the upper margin of the vertebral foramen. In the upper part of the cranial articular facet, apart from the craniomedial, there is also the ventral component of its direction, in contrast to dorsal one, prevailing in the lower part.

During the vertical slipping of the cranial articular facet of atlas over the occipital condyle surface in

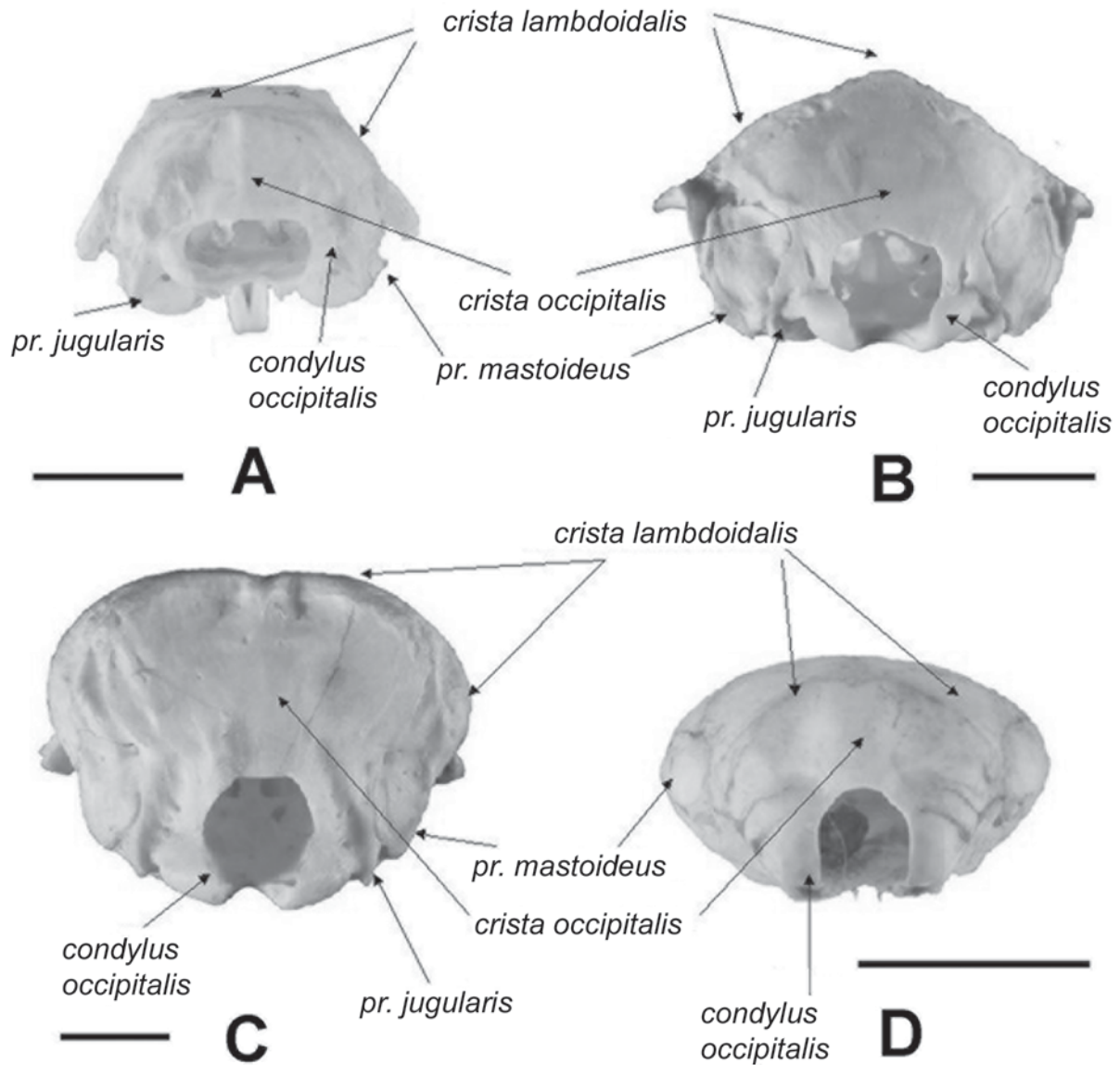


Figure 4. The occipital region of the skull in caudal view.

A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*. Scale bars are 1 cm.

Rattus, their most coincidence is observed in the middle and more ventral regions of the condyle when the rat head is lowered. In such position the maximum working stress falls on the occipital joint (Sukhanov & Manzii, 1986). Such head position is likely the most convenient for the animal and often used during the animal's activity, including prospecting the new territory and search for food. The amplitude of the atlas vertical translations in occipital joint of *Rattus* is about 80° (Tab. 1). In the extreme upper and lower atlas positions on the condyles surface the durable fixation of its conditions is observed, while in intermediate phases of the vertical slipping there is a possibility of lateral displacements, to the extent of about 26° . The structural peculiarities of the occipital condyles and cranial articular surfaces of atlas in *Rattus* make possi-

ble the maximum mobility in this joint just in intermediate and more ventral positions of the latter. Meanwhile, more dorsal positions of the atlas are possible too but probably less efficient.

In *Spalax* and *Nannospalax* the cranial articular facet of atlas is also kidney-shaped, but deeper than in *Rattus* (Fig. 7B). Dorsally it does not project beyond the upper margin of the vertebral foramen. On the whole, the cranial component of its direction is expressed more significantly as compared to that in *Rattus*. At vertical slipping of the cranial articular facet over the occipital condyle surface a high extent of the coincidence is retained practically at all atlas positions. The amplitude of the atlas vertical translations in *Spalax* is about 115° , and in *Nannospalax* it varies from 130° to 140° , that is significantly greater than in *Rattus*

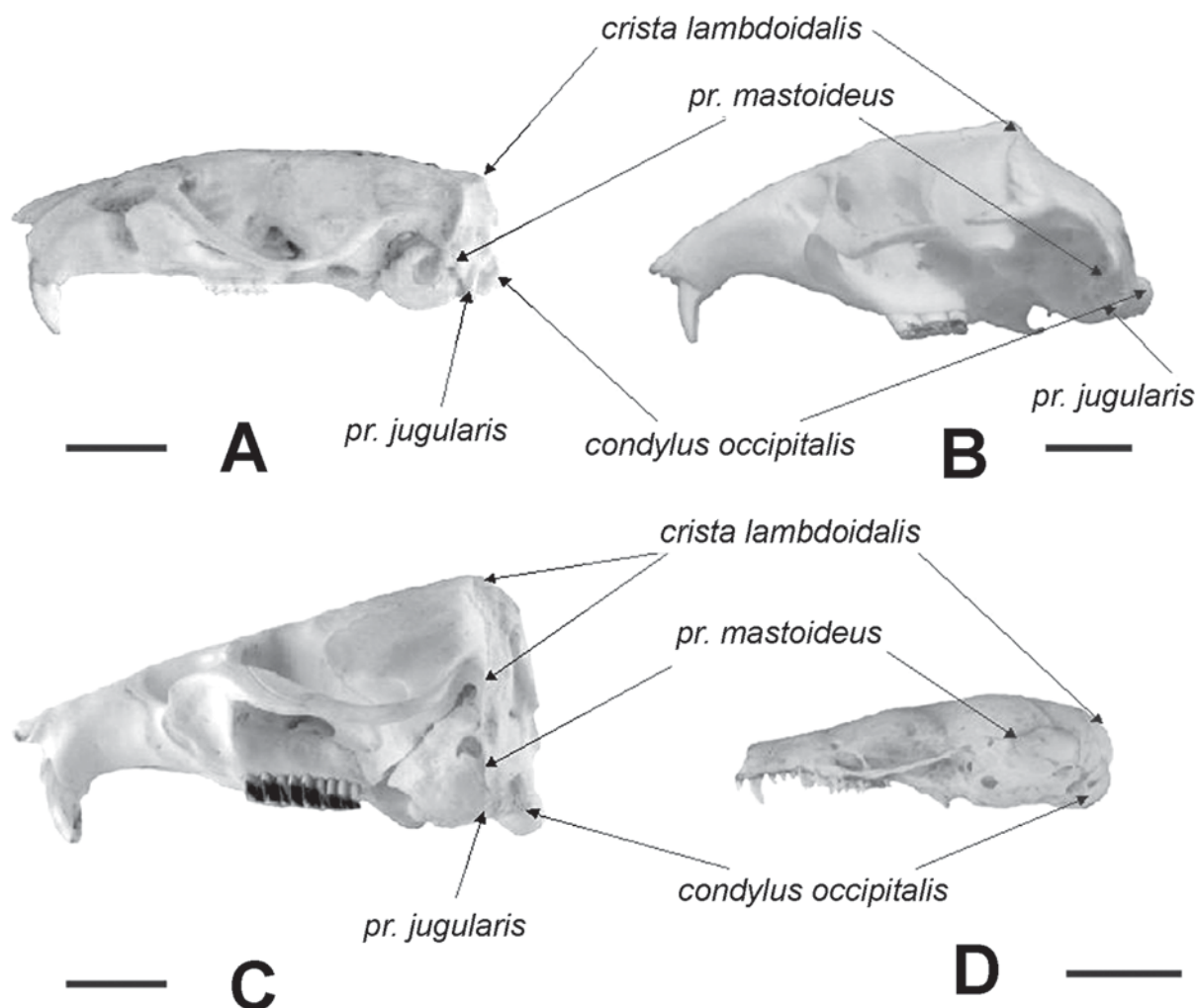


Figure 5. The occipital region of the skull in lateral view.

A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*. Scale bars are 1 cm.

(Tab. 1). Furthermore, in both forms the possibilities of the atlas lateral displacements increase too, since these motions are restricted only in the extreme lower position of the latter. In the extreme upper atlas position some mobility in lateral directions is retained, however its whole spread in *Spalax* is narrower than in *Nannospalax* and *Rattus* (Tab. 1). The peculiarities of the occipital joint mobility in *Spalax* and *Nannospalax* reflect the specific character of their burrowing activity which is connected with the throwing the soil with the head. In this case all the phases of the head lifting (from the extreme lower to the extreme upper positions) are the strongly load-carrying (Gasc *et al.*, 1986).

In *Myospalax* the form and structure of the cranial articular facet of atlas is very similar to that in *Spalax*. At the same time its upper part is more widened and rounded, and on the ventral arch between the facets there is a small eminence (Fig. 7C). In *Myospalax* as in *Spalax* the significant coincidence of articular surfaces of atlas and occipital condyles is observed. However, in

contrast with *Spalax*, the extreme upper atlas position is fixed on the skull as well as its extreme lower position. In the first case the upper margins of the atlas articular surfaces are butted up against depressions on the basio-ccipital, and the cranial bifurcate ridge of the atlantal neural arch extends beyond the foramen magnum. At extreme lower atlas position the thickening of its lower arch fits in a special depression on the ventral side of the skull. The amplitude of the atlas vertical translations in *Myospalax* is slightly inferior to that value in *Spalax*, and the spread of its lateral displacements is similar too (Tab. 1). The latter are possible in the intermediate atlas positions mainly, however, in contrast to that of *Spalax*. The insignificant lateral mobility of atlas is preserved in its extreme upper position on the occipital condyles. The structural and functional peculiarities of the occipital joint in *Myospalax* as in *Spalax* and *Nannospalax* are apparently connected with a predominance of the strongly load-carrying conditions during all phases of the head lifting at throwing the soil

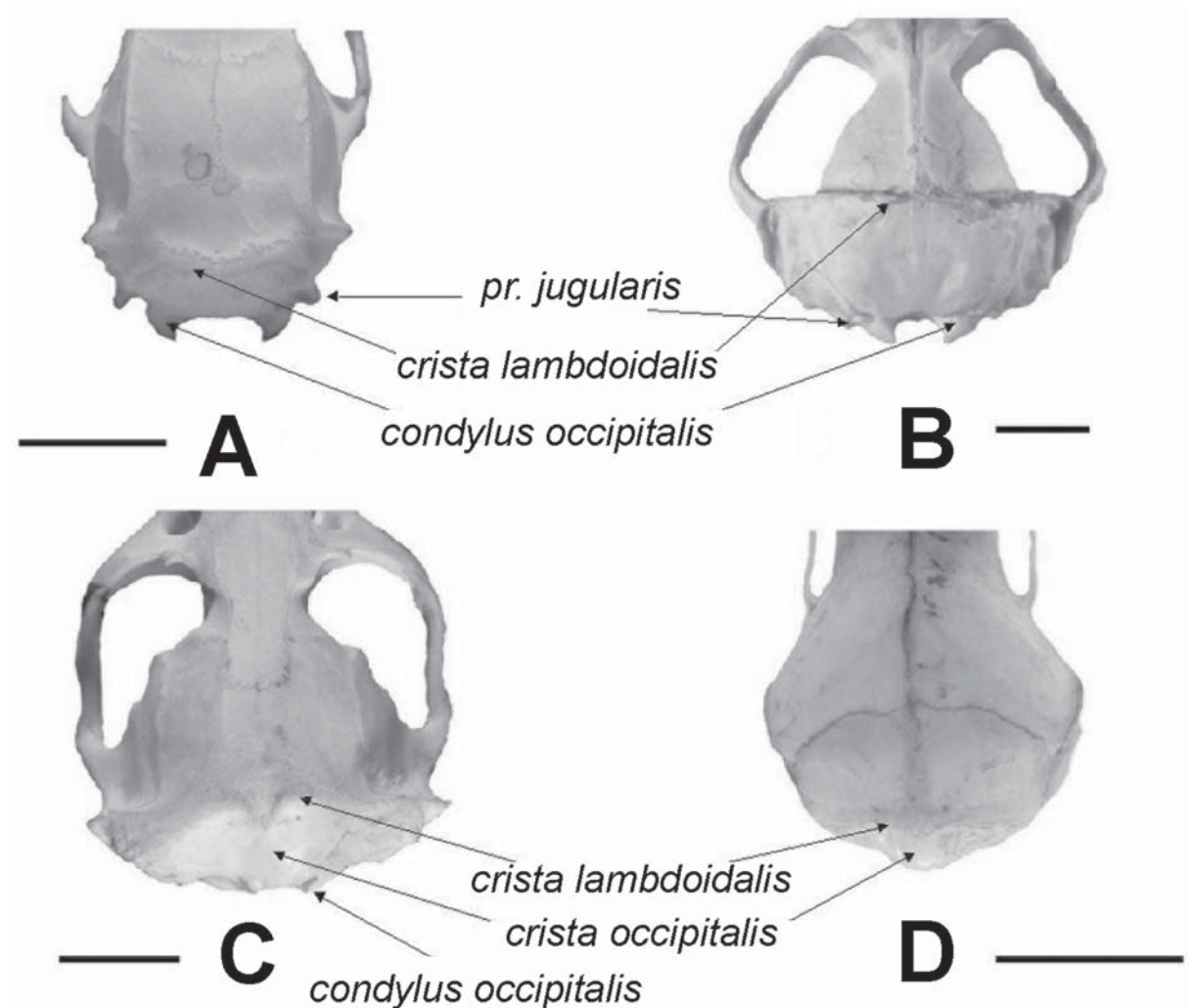


Figure 6. The occipital region of the skull in dorsal view.

A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*. Scale bars are 1 cm.

Table 1. Some functional characteristics of the occipital and atlanto-axial joints. The average values for the angles:

1) slope of the occipital condyles to the palatine plane; 2) vertical displacement of atlas in the occipital joint; 3) lateral displacement of atlas in the occipital joint; 4) rotation of atlas around the axis in the atlanto-axial joint.

species	1	2	3	4
<i>Rattus norvegicus</i>	40°	80°	26°	120°
<i>Spalax microphthalmus</i>	23°	115°	22°	70°
<i>Nannospalax nehringi</i>	25°	135°	25°	80°
<i>Myospalax myospalax</i>	33°	112°	20°	80°
<i>Talpa europaea</i>	60°	70°	24°	35°

away in process of digging (Gasc *et al.*, 1986; Gambaryan & Gasc, 1993).

In *Talpa* the cranial articular facet of atlas has an expanded upper part which, however, is less than half

as great as its length in contrast to that of all other forms mentioned above (Fig. 7D). Therefore, the form of the atlas articular surfaces in *Talpa* cannot be described as kidney-like. Their ventral parts likewise are slightly expanded. As a whole, the horizontal component is absent in the articular surface direction, while it is characteristic of the facets direction in other forms studied. The cranial component of the direction dominates over the whole course of the cranial articular facet movement although the slight medioventral turn is evident in its upper part and the slight dorsal in the lower one. At the vertical atlas slipping over the occipital condyles the coincidence of their articular surfaces is just below in its extreme upper position. In this case the dorsal tubercle of the upper arch can extend on the basioccipital fixing the atlas position. At the same time, the extreme lower atlas position is fixed by going beyond of the lower atlas arch in a special depression on the ventral skull surface. Owing to the flattening of the condyles in *Talpa* the rotation axis of the occipital joint

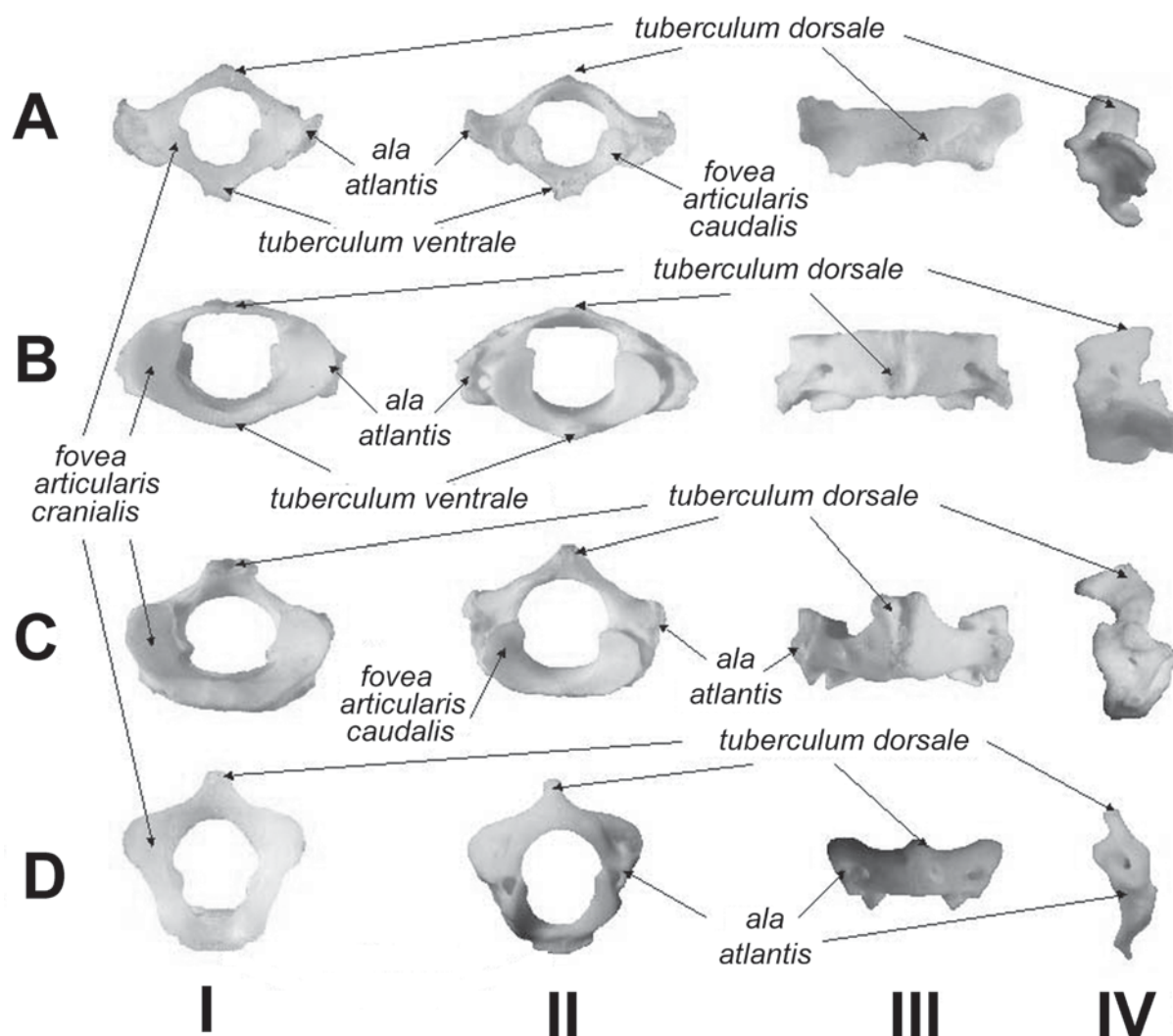


Figure 7. Atlas in cranial (I), caudal (II), dorsal (III), and lateral (IV) views.

A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*.

is disposed as if it was inside the skull, while in rodents studied it is located inside the occipital condyles themselves, since the latter are convex sufficiently and project strongly beyond the foramen magnum margins (Fig. 5). The amplitude of the atlas vertical translations in *Talpa* is about 70° and somewhat less than such in *Rattus* (Tab. 1). Its lateral displacements are possible in the intermediate (between of the extreme upper and lower) positions only and their magnitude is close to that in other forms studied.

Atlanto-axial joint

Atlas. In *Rattus* the atlas is strongly flattened dorsoventrally, so that the width of the vertebral foramen is larger than its height (Fig. 7). In the row *Spalax* (*Nannospalax*) – *Myospalax* – *Talpa* the overall proportions of the atlas change gradually with increasing of the vertical component. Thus, in *Talpa* the width of the

atlas is equal to its height and the height of the vertebral foramen is greater than its width.

The upper arch of atlas in *Rattus* is more massive and about 2–2.5 times wider than its lower arch (Fig. 7). In *Spalax* the similar proportions are observed, while in *Nannospalax* and *Myospalax* the upper arch is wider too but to a lesser degree than in two latter forms. At the same time, the ventral arch in these burrowing forms becomes thicker in comparison with the dorsal arch. In *Talpa* the lower arch is narrower than the upper arch but dorsoventrally wider.

On the external surface of the atlantal dorsal arch there is the dorsal tubercle which in *Rattus* is not tall and pointed to a different extent (Fig. 7). Generally it is asymmetrical and displaced forward a little to the thickened cranial margin. In *Spalax* and *Nannospalax* the dorsal tubercle is also asymmetrical but displaced to the thickened caudal margin of the dorsal arch. In *Myospalax* the dorsal tubercle is located nearly on the

centre of the dorsal arch and extends cranially into the characteristic bifurcated prominence on its cranial margin. In *Talpa* the dorsal tubercle is well developed and as in *Rattus* is situated on the cranial margin of the dorsal arch, and directed craniodorsally (Fig. 7).

The ventral tubercle on the atlantal ventral arch in *Rattus* is strongly projected and looks like the short caudoventrally directed process (Fig. 7). In *Nannospalax* the ventral tubercle has similar construction, but the process on the posterior margin of the arch is directed caudodorsally. In *Spalax* the ventral tubercle is weakly developed, in *Myospalax* it is hardly noticeable and in *Talpa* it is practically absent. On the inside (dorsal) surface of the ventral arch in all forms studied the special articular area for the dens of axis is located. In *Rattus*, *Spalax*, and *Nannospalax* in front of the ventral arch there is a groove and in *Myospalax* a small projection, providing the atlas fixation in its extreme lower position on the ventral part of the skull. In *Talpa* for this purpose on the ventral arch there is a special ventral plate directed caudoventrally.

The atlantal wings (=transverse processes) in *Rattus* are the rather wide plates, inclined from the front to back in caudoventral direction at an angle of 30–45° to the horizontal plane, with more thickened posterior parts (Fig. 7). Dorsally the atlantal wings do not reach the level of the upper margin of the vertebral opening and caudally they are separated by narrow groove from the posterior articular facets. From above, in the region of this groove there is the transverse foramen for the arteria vertebralis. The latter passes also through the hardly noticeable opening on the ventral side of the atlantal wings, on the bottom of the specified concavity (fossa atlantis). On the dorsal surface of the atlantal wings the pair of the large openings (alar foramina) is well seen, which serve for the vessels and nerve and lead to the transverse canal. The latter is opened also by the intervertebral foramen (=foramen vertebrale laterale) on the ventral side of the dorsal arch. In some specimens of *Rattus* the deepening of the shallow notches on the anterior margin of the upper arch is observed.

In *Spalax* the general plan of the atlas wings structure and direction is similar to that of *Rattus*, however, the notches behind them are narrower (Fig. 7). In *Myospalax* the atlantal wings are strongly short-cut in comparison with those of preceding forms. Meanwhile, their distal extremities are thickened significantly (especially anteriorly) and situated nearly parallel to the horizontal plane. In *Talpa* the atlas wings are almost concealed, with slight caudal thickening.

The caudal articular facets for the articulation with axis in *Rattus* are smaller than cranial facets, with rounded dorsal parts and sharply narrowed ventral margins (Fig. 7). Their dorsal margin is placed approximately at the level of the middle of the vertebral foramen height. In *Spalax* and *Nannospalax* the caudal articular facet is of the triangular form dorsally and gradually narrowed ventrally. In *Myospalax* the total form of the caudal facets looks horseshoe-like, with the

fovea dentis at the middle. In *Talpa* there is only vertical component of this “horseshoe”.

Axis. In *Rattus* the vertical axis of the spinous process of the axis inclines backwards at an angle of 60–65° to its longitudinal axis (Fig. 8). The height of the plate-like spinous process is slightly less than the height of the remaining part of the vertebra and its basis is somewhat thickened. The upper border of the spinous process is slightly convex and strongly splay in front (at an angle of about 40° to the longitudinal axis of the vertebra); it is gradually thickened caudally, forming the crista epistrophei. The thickened posterior border of the process in its dorsal part projects noticeably backwards, leaning partly on the spinous process of the third cervical vertebra. Anteriorly, an analogous rounded prominence in the basis of the axis spinous process can slightly overhangs the atlas dorsal arch.

In *Spalax* the inclination extent of the neural arch and craniodorsal border of the spinous process is similar with those in *Rattus*, while in *Nannospalax* the position of this process is more vertical, with the slope of about 60° (Fig. 8). Meanwhile, the spinous processes in these forms are more massive and their height is almost equal to that of the remaining part of the axis. Their crista epistrophei is strongly thickened and forms posteriorly on the apex two lateral projections which are larger in *Spalax*. The caudal border of the spinous process in both forms has the deep furrow and leans on the spinous process of the third cervical vertebra as in *Rattus*. The forward thickened prominence in the basis of the spinous process in *Nannospalax* is developed stronger than in *Spalax* but weaker than in *Rattus* and in both burrowers hardly reaches the level of the posterior border of atlas dorsal arch.

In *Myospalax* the axis fuses usually with two following vertebrae (Fig. 8). Their centra and neural arches are involved in the fusion but transverse processes are separate. As a result the overall neural arch and its spinous process amplify greatly, and the latter is directed dorsally in contrast to its dorsocaudal direction in preceding forms. The height of the spinous process is somewhat greater than the height of the remaining part of the axis. The crista epistrophei is thickened and divided into two lateral paddles which, in contrast to that of *Spalax* and *Nannospalax*, weakly project. On the dorsocranial margin of the crest a small notch is observed. The anterior prominence in the basis of the crest strongly projects beyond the cranial margin of the axis neural arch and reaches the level of the posterior border of the atlas dorsal arch.

In *Talpa* the vertical axis of the neural arch is almost perpendicular to the longitudinal axis of vertebra (Fig. 8). The spinous process is weakly developed; its height is approximately two times less than the height of the remaining part of vertebra. It extends posteriorly so its caudal part overhangs the spinous process of the third cervical vertebra and reaches the boundary between third and fourth cervical vertebrae. At the articulation with atlas the anterior prominence is well developed in

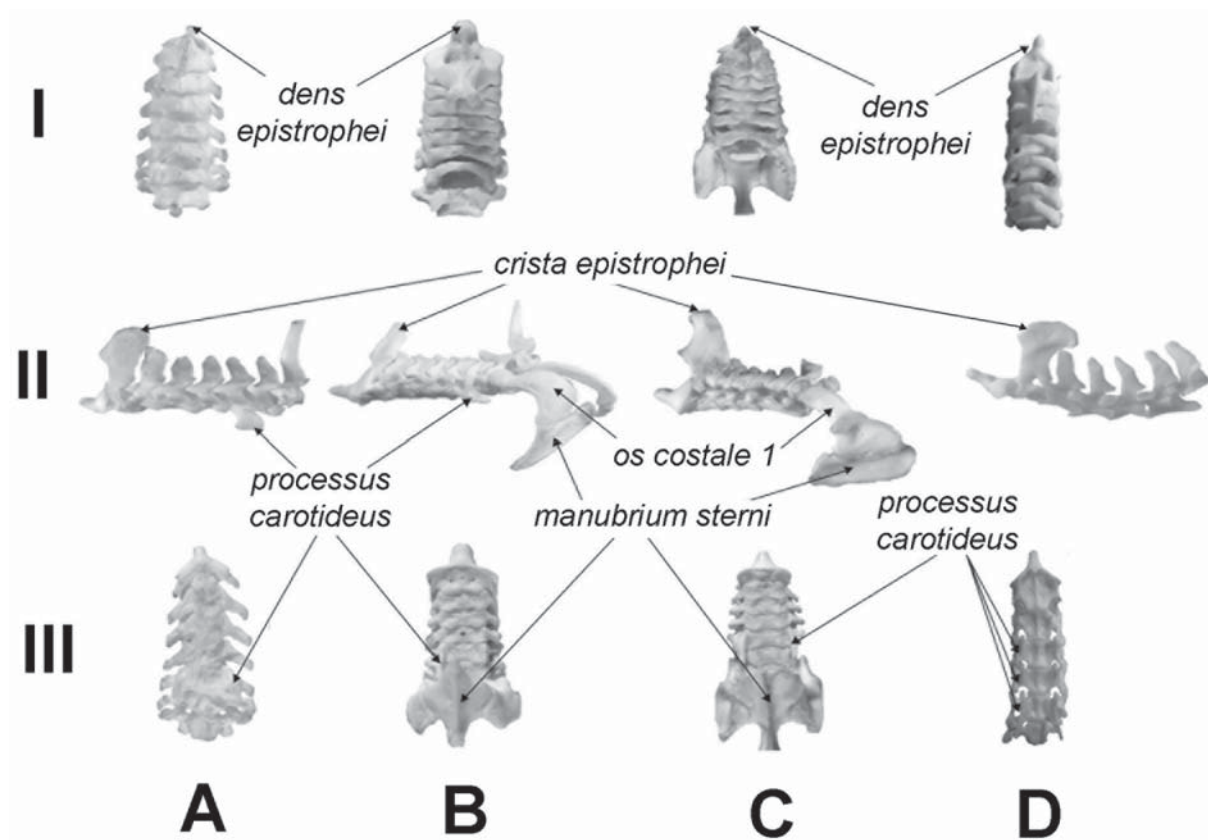


Figure 8. Cervical and anterior thoracic vertebrae in dorsal (I), lateral (II), and ventral views (III). A — *Rattus norvegicus*; B — *Spalax microphthalmus*; C — *Myospalax myospalax*; D — *Talpa europaea*.

the basis of the axis crest and it usually overhangs strongly the atlas dorsal arch.

The dens of axis in *Rattus* is deflected dorsally at an angle of about 15° to the longitudinal vertebra axis. It is not strongly prominent anteriorly and constitutes approximately a half of the vertebral centrum length. The ventral surface of the dens is smooth and contacts with the fovea dentis of atlas which extends up to the anterior border of its ventral arch. The dorsal surface of dens is rough and serves for the attachment of its transverse ligament. Caudally on the dens sides two convex articular cranial facets are situated. Their surfaces are oval-shaped and craniolaterally directed. The peculiarities of the atlas-axis joint in *Rattus* ensure the high extent of the vertebrae mobility: the significant (up to 120°) amplitude of the atlas rotation and some (several degrees) vertical and lateral its deflections (Tab. 1).

In *Spalax* and *Nannospalax* the dens of axis projects beyond the vertebral centrum margin more than in *Rattus* and its length is approximately equal to that of the axis centrum. The dens is dorsally deflected at a greater angle (about 35°) than in *Rattus* (Fig. 8). The dens of axis contacts with the fovea dentis of atlas up to the half of its ventral arch wide, where the attachment of the joint pouch of the occipital joint is observed.

The cranial articular facet of axis in *Spalax* and *Nannospalax* is of oval or kidney shape, flatter than in *Rattus* and mainly turned round cranially with very weak lateral component. Its width is almost identical to that of the fovea articularis caudalis of atlas. The lower margins of the anterior articular facets look like the crest, which protrudes strongly over the ventral surface of the vertebral centrum. Under the dens of axis in *Nannospalax* there is also the narrow articular surface over which the cranial process of the atlantal ventral arch slides during the rotation. All the peculiarities mentioned above result in practically the full limitation of the vertical and lateral mobility in atlanto-axial joint in *Spalax* and *Nannospalax* in comparison with that of *Rattus*. The amplitude of the atlas rotation in these forms is also significantly smaller than such in *Rattus* (about $70\text{--}80^\circ$; Tab. 1).

In *Myospalax* the proportions in the dens structure are nearly identical to those in *Spalax*. However, its basis is relatively wider and its tip is dorsally deflected at greater angle (about 40° ; Fig. 8). The articulation with the fovea dentis of atlas is similar to that of *Spalax* but area of the contact is larger. It is connected with the expansion as the fovea dentis as the ventral articular region under the dens which joins the anterior articular

facets. Their lower borders look crest-like and protrude strongly over the surface of axis centrum as in *Spalax*. The cranial articular facet in comparison with that of *Spalax* is wider medially and more convex. In its direction the lateral turn increases and the dorsal component arises. Its width is slightly greater than the width of the fovea articularis caudalis of atlas. As a result in *Myospalax* there is possibility for some vertical and lateral atlas displacements and the maximum amplitude of the rotation is nearly identical to that of *Nannospalax* and *Spalax* (Tab. 1). The atlas rotation in its extreme upper position is noted too but it is more limited (about 50°).

In *Talpa* the length of dens of axis is less than in forms described above, little more than half of the axis centrum length. The width of the dens basis corresponds nearly exactly to the width of the lower part of the atlantal vertebral foramen as it is observed in *Spalax*, *Nannospalax*, and *Myospalax*. An angle of the dens inclination to the longitudinal vertebra axis is less than in *Spalax* (about 30°; Fig. 8). At the articulation with the atlas the axis dens has support on the very narrow, almost vertical fovea dentis.

The anterior articular surfaces of axis in *Talpa* are triangular in form and rather convex with most pronounced lateral component of their direction in comparison with those of all other forms mentioned above (Fig. 8). The ventral articular region, uniting both articular facets ventrally, is developed as well as in *Myospalax*. On its surface there is a caudoventrally directed process. The structural peculiarities of the atlas-axis joint in *Talpa* result in the negligible extent of the atlas rotation (35°) but a more distinct vertical mobility as in *Rattus* (Tab. 1).

The caudal articular facet of axis for the articulation with the third cervical vertebra in *Rattus* is narrower than the cranial articular facet and is facing caudoventrally. In *Spalax* and *Nannospalax* it is facing in the same direction and in *Talpa* it faces more ventrally. In *Myospalax* the axis fuses with three subsequent cervical vertebrae.

On the ventral side of the axis centrum in *Rattus* there is a central crest. In other forms studied this crest is absent while in *Talpa*, on the contrary, there is a concavity on its place. The caudal articular surface of the axis centrum in *Rattus* is inclined posteriorly at an angle of about 45° and has the joint pouch for the articulation with the centrum of the following cervical vertebra. In *Spalax*, *Nannospalax*, and *Talpa* the similar situation is observed.

The transverse processes of axis in *Rattus* are relatively thin, narrow and their pointed tips are caudolaterally and slightly dorsally directed; at their basis there are intervertebral openings (transverse foramen). The transverse process is separated from the postzygapophysis by a deep notch (incisura vertebralis caudalis). On the anterior border of the neural arch the wide notch is situated too (incisura vertebralis cranialis). In the burrowing forms the structural plan described above is mainly retained, but in *Spalax*, *Nannospalax*, and *Talpa* the extremities of the transverse processes are al-

most concealed. In *Myospalax*, in connection with the fusion of the second to fourth cervical vertebrae the transverse process is more short and thin.

Third to seven cervical vertebrae

These vertebrae are characterized by rather similar structure except the sixth and seventh vertebrae which differ by some specific features (Fig. 8).

The vertebral centra in *Rattus* are flattened dorsoventrally and their articular surfaces are posteriorly inclined at an angle from 30° (third–fourth cervicals) up to 50–60° (sixth–seventh cervicals) to the longitudinal axis of vertebra. The posterior articular surface of the seventh vertebra centrum is almost perpendicular to the longitudinal axis of spine. The posterior articular surface of the each preceding vertebra articulates with the anterior articular surface of the successive one by a very thin intervertebral disc. The cervical vertebrae are the shortest vertebrae of the vertebral column. The length of their centra differs a little but fourth and fifth (sometimes sixth) vertebrae are sometimes shorter than the other. The last cervical vertebra has on the posterior end of the centrum facet for the head of the first rib.

In adult specimens of *Myospalax* and *Spalax* the fusion of cervicals is quite often takes place (Fig. 8). In *Myospalax* the second to fourth cervicals and in *Spalax* the fourth to sixth cervicals generally fuses, while in other spalacids this phenomenon is not observed. The splay character of the articular surfaces of the vertebral centra in the majority of the burrowing forms studied is slightly differs from the condition of *Rattus*. In *Talpa* the smooth vertical curve (at an angle of about 150°) in the vertebral centra arrangement, starting from the fourth–fifth cervical vertebrae is observed.

The neural arches of the cervical vertebrae in *Rattus* are high and wide. However, starting from the axis, there is a tendency to their narrowing and simultaneously to the flattening and gradual widening of the vertebral foramen up to the sixth–seventh cervicals. On the plate of the neural arch of the third cervical there are generally small, sometimes indistinct openings, which are absent in the successive vertebrae. The regions between neural arches (spatium arcuale) are rather wide. The anterior and especially the posterior vertebral notches (incisura vertebralis cranialis et caudalis) are well pronounced. All these peculiarities facilitate mobility of the elements of the cervical section. Meanwhile, all the vertebrae are firmly connected by powerful ligaments by means of which a necessary hardness is provided on this part of the vertebral column.

In *Spalax*, *Nannospalax*, and *Myospalax* the plate of neural arch of the seventh cervical is narrower than that in the preceding vertebrae. The openings on the third vertebra in *Spalax* and *Nannospalax* are not distinct, whereas in *Myospalax* there are one-two foramina on each side of the fused arches of second to fourth vertebrae. The vertebral notches, especially in *Spalax*, are developed somewhat weaker than in *Rattus*. In

Talpa in the anterior part of the cervical series (third to fifth vertebrae) the neural arch is narrowing, while in the posterior part of the series it is widening. In that case the spatium arcuale can be rather wide that makes possible the significant vertical mobility in cervical section. The vertebral notches (especially anterior) are more pronounced in *Talpa* than in preceding forms.

In *Rattus* the spinous process is gradually shortens from third to fifth cervicals and it is weakly developed on the last four cervicals, where its height is approximately equal or gradual increases to the seventh cervicals. Sometimes, the change in the direction of spinous processes is observed. It is generally dorsocaudally directed on third–fourth cervicals and dorsocranially directed on the last vertebrae. In *Spalax* as in *Rattus* the tendency to the shortening of the spinous processes from third to sixth cervicals is noted; their direction is indistinct, rather dorsocranially; on two last vertebrae the spinous processes are not distinct. In *Nannospalax* the spinous process of the third cervical is also the most developed. In *Myospalax* even with the fusion of the second to fourth cervicals the spinous process of the fourth cervical is well developed, whereas on the following three vertebrae the processes are almost unnoticeable. In *Talpa* the spinous process is more distinct on the third and seventh cervical vertebrae and on the latter it is dorsocaudally directed as in the first thoracic vertebra.

The zygapophyses in *Rattus* are widely separated. The prezygapophyses are more raised with relatively wide but flat facets. The latter are mainly dorsomedially directed with some cranial component. In *Spalax*, *Nannospalax*, and *Myospalax* in the direction of prezygapophyses the cranial component is more pronounced and the distance between their centers increases gradually from the third to seventh cervical vertebrae. Meanwhile, in these burrowers, unlike the *Rattus*, the facets of the prezygapophyses on all unfused vertebrae are concave and divided into two part, anterior and dorso-posterior, meeting at a transverse groove. In *Myospalax* on the sixth–seventh vertebrae the anterior, more convex facet parts are bigger than posterior ones and have more pronounced dorsal components. In *Spalax* and *Nannospalax* the similar structure is observed on the seventh cervical vertebra only and on the remaining vertebrae the anterior part of the facet is flat and approximately equal to the dorsoposterior part in size.

In *Talpa* the articular facets of the prezygapophyses are dorsomedially directed as in *Rattus* and towards the end of the cervical series their dorsal component increases. In this case, in contrast to three preceding forms, the cranial component is practically absent, but this component exists owing to the vertical curve in the cervical section (starting from the fourth–fifth cervicals; Fig. 8). The distance between the prezygapophyseal centers changes negligibly backwards the series. The convexity of the anterior articular facets, especially on the fifth–sixth cervicals, is also noticeable.

The postzygapophyses in *Rattus* are almost not distinct; their facets are comparatively flat and situated at

the level of the neural arch pedicels and their direction is mainly caudoventral with some lateral turn (on the sixth–seventh vertebrae these processes are inclined more ventrally). The postzygapophysis is separated from the pleurapophysis by rather deep posterior vertebral incisura. In this case the levels of the facets position nearly coincide. In *Spalax* and *Nannospalax* the postzygapophyses are more pronounced on the sixth–seventh cervical vertebrae. In contrast to those in *Rattus* their articular facets are more convex and in their direction the caudal component is more prominent. In *Myospalax* the structure and the direction of the postzygapophyseal facets is similar to that in preceding forms. However, the processes themselves are weakly developed as in *Rattus*. In *Talpa* the analogous situation is observed but articular facets are concave and the ventral component predominates in their direction.

The pleurapophyses in all forms mentioned above arise from two roots originating from the centrum and arch of the vertebra. These two branches are joined and form intertransverse opening (foramen transversarium), the axis of which passes along the vertebral centra; on the seventh cervical vertebra it is absent.

In *Rattus* the pleurapophysis of the third cervical vertebra deviates posteriorly (at an angle of 30–40° to the longitudinal axis of vertebra) and can form the small prominence anteriorly. On the following vertebrae an angle of the pleurapophysis deviation increases up to 70–80° and more.

In *Spalax* and *Nannospalax* the pleurapophyses are significantly shorter than those in *Rattus* and their tips deviate posteriorly at the similar angle with the exception of the sixth and seventh vertebrae. The processes of the latter are directed more perpendicular to the longitudinal axis of vertebrae. As a result the approaching or, sometimes, fusion of the distal widenings of pleurapophyses on the fifth–sixth (in *Spalax*) or on the (fifth) sixth–seventh (in *Nannospalax*) cervical vertebrae and the formation of the total, wider surface is observed. This results in the limited mobility of the cervical vertebrae, functioning as a single whole. The distal extremities of pleurapophyses on the remaining cervical vertebrae are less widened. In *Myospalax* there is a similar situation with respect to the direction of the pleurapophyses on the sixth vertebra, however, the approaching of their extremities with those of the adjacent vertebra is not observed. On the whole, the pleurapophyses in *Myospalax* are better developed than in *Spalax*; their length and width on the tips increase slightly from front to backwards. Meanwhile, as in *Spalax* and *Nannospalax* and in contrast to that in *Rattus*, the pleurapophysis of the seventh cervical vertebra in *Myospalax* does not participate in the formation of the common articular surface along with the diapophysis of the first thoracic vertebra for the articulation with the tuberculum of the first rib. However, the extremity of the pleurapophysis of the last cervical vertebra approaches closely enough to the articular facet of the diapophysis of the first thoracic vertebra, inserting to its border by the special ligament.

In *Talpa* the pleurapophyses are in the form of thin lamellar processes and well developed on the third–fifth cervical vertebrae only, their extremities being posteriorly directed with some ventral deviation. On the sixth cervical vertebra these processes are practically not distinct and again noticeable on the seventh cervical as some prominences on the neural arches pedicel. The distance between the extremities of the pleurapophyses (except the sixth–seventh cervical vertebra) in *Talpa* is less than between ones of the postzygapophyses that is due to the unusual direction of these lamellar processes which are somewhat medially instead of laterally directed as in other species studied.

In all species investigated on the sixth cervical vertebra there are particular ventral crests which extends from the bases of the pleurapophyses. This is lamellar process of Howell (1926), pr. carotideus of Green (1935), or crista ventralis processu transversarii, or pr. carotideus of Pilipchuk (1993). These wide lamellar processes are ventrolaterally and somewhat caudally directed but do not generally project beyond the sixth cervical vertebra. In one specimen of *Rattus* the similar lamella was also developed on the fifth vertebra but on the left side only, where it was accreted with the ventral crest of the sixth vertebra.

In *Spalax* and *Nannospalax* the ventral crests are also developed on the sixth vertebra but in contrast to the condition of *Rattus* the caudal component predominates in their direction and these lamellas extend posteriorly beyond the region of the sixth vertebral centrum. In *Myospalax* the structure and direction of the crista carotideus are similar to that of *Spalax* but they are somewhat longer, reaching almost the posterior border of the seventh vertebral centrum.

In *Talpa* the ventral crests on the sixth cervical vertebra are also well developed but look like rather the thin plates than the processes. In contrast to those of the preceding forms, there are both caudal and cranial components in their direction. The posterior extremities of the ventral crests extend beyond the bound of the sixth vertebral centrum and the anterior ones reaches the level of the bound with the fifth vertebra. The similar lamellar processes in *Talpa* are also observed on the fourth–fifth cervical vertebrae and directed cranioventrally. In this case the processes of the fourth cervical vertebra usually contact with the pleurapophyses of the third vertebra, forming the peculiar block.

Köhl (1917) supposed that ventral crests serve for the increase of the hardness in the cervical section which is necessary during the burrowing and swimming of animals. According to our opinion, the development of the ventral processes is connected not only with the ensuring of hardness, but also with the increasing of the force attachment lever of m. longus colli. It is just in the region of sixth vertebra the thoracic part of this muscle, inserting on the caudal area of these lamellas, transfers to the cervical part, attaching to their cranial area. In *Talpa* the strengthening of the cervical part of m. longus colli results in the arising of analogous lamellar processes on the fourth–fifth cervical vertebrae.

The structural peculiarities of the cervical vertebrae listed above indicate the differences in their mobility in forms investigated. On the third–seventh vertebrae in *Rattus* the possibility of some vertical and lateral displacements is noted. It is obviously connected with the structural and disposition features of the articular facets of zygapophyses. In the latter the dorsoventral components of their direction are more pronounced; the characteristic relief of the surfaces (plane or somewhat convex in prezygapophyses and concave in postzygapophyses) and the definite difference in the size of articulation areas (the prezygapophyseal facets are wider generally) are also observed.

In *Talpa* the structure of the articular facets of the zygapophyses is somewhat different from that in *Rattus*: in their direction the dorsoventral component is more marked and craniocaudal component is practically lost; the articular surfaces are comparatively narrow and more convex in the prezygapophyses and more concave in the postzygapophyses. As a result the cervical vertebrae in *Talpa* are characterized by the significant vertical mobility but the lateral displacements are practically absent.

The articulation character of the cervical vertebrae in *Spalax*, *Nannospalax*, and *Myospalax* is mainly similar. The significant concavity of the articular surface on the prezygapophyses (and respectively their convexity on the postzygapophyses) as a result of their characteristic curve and the more distinct display of the craniocaudal orientation of the facets leads to the whole prohibition of the lateral displacements of the vertebrae. Meanwhile, in *Myospalax* the some vertical mobility at the articulation of the fifth–seventh vertebrae and in *Spalax* and *Nannospalax* of the sixth–seventh cervical vertebrae are possible nevertheless.

Peculiarities of the thoracic vertebral morphology

In the thoracic section the dorsal surface of the first seven–eight vertebrae is the mostly interesting for us as a region of the attachment of muscles which are responsible for the head lifting. In this connection many details of the thoracic vertebrae structure were not examined.

The first thoracic vertebra in *Rattus* resembles greatly the cervical vertebrae and the last three–four thoracic vertebrae resemble the lumbar vertebrae. The centrum length of the thoracic vertebrae in *Rattus*, *Spalax*, *Nannospalax*, and *Talpa* increases gradually in caudal direction. As a result the last (13-th) vertebra may be noticeably (approximately 1.5 times) longer than the first one. In *Myospalax* the centrum length changes slightly but it increases on the second and on the last three thoracic vertebrae. In *Talpa* there are the sesamoids between the vertebral centra, starting from the 10–12-th thoracic vertebrae; the latter gradually increase in size in caudal direction (Dobson, 1882; Platonov, 2002).

Table 2. Some morphofunctional characteristics of the second to tenth thoracic vertebrae: 1) slope angle of the spinous processes; 2) ratio of width of the spinous process tip to the width of its base, in %; 3) ratio of the height of the spinous process to the whole height of the vertebra, in %.

vertebra	Rattus			Nannospalax			Myospalax		
	1	2	3	1	2	3	1	2	3
II	82°	67	62	76°	28	54	57°	50	64
III	65°	37	46	58°	20	48	47°	83	66
IV	60°	34	45	49°	51	43	39°	93	69
V	55°	44	50	19°	50	47	39°	70	66
VI	43°	45	46	24°	44	47	39°	56	64
VII	47°	64	48	25°	36	52	45°	65	65
VIII	47°	70	54	32°	71	51	44°	100	58
IX	47°	70	34	38°	72	39	44°	100	51
X	62°	64	34	40°	60	29	52°	104	48

In all forms investigated the neural arch of the thoracic vertebra joins with the vertebral centrum by the thickened pedicles, on the anterior and posterior margins of which there are paired incisura vertebralis cranialis et caudalis, the latter being significantly deeper. The notches of the adjacent vertebrae form the comparatively narrow, horizontally elongated intervertebral foramen for the spinal nerve. To the end of thoracic section the size of these openings decreases, partly owing to the decrease of the anterior notch depth.

The width of the arcus vertebrae lamina in *Rattus*, *Spalax*, and *Talpa* increases gradually in caudal direction and on the last thoracic vertebra it nearly three times exceeds that of the first vertebra. In the same direction the displacement of the lamina arcus vertebrae with respect to the vertebral centrum is also observed. On the caudal margin of the dorsal lamina of the first-sixth thoracic vertebrae there are small but wide notches and also triangular notches, on the cranial margin of lamina of the 7th – 11-th vertebrae. In *Nannospalax* the width of the dorsal lamina on the last thoracic vertebra exceeds that of the first vertebra more than four times and in *Myospalax* approximately 2.5 times.

The spinous process of the first thoracic vertebra in *Rattus* is weakly developed and differs insignificantly from that of the last cervical vertebra. Meanwhile, the spinous process of the second thoracic vertebra is strongly enlarged and highest of the all vertebral column; it is almost vertically directed. It looks like an elongated rectangle in its transverse section and amplifies equally both to its basis and its tip. On the extremity of the spinous process there is a joint with the triangular bone lamina anteriorly directed. On its ventral side the attachment of several ligaments passing to the spinous processes of the cervical vertebrae is observed. Thus, “the amortization organ” of the vertebral column is formed (Gambaryan, 1951, 1972, 1974). In the center of the caudal surface of this spinous process there is a small crest and anterior to the process basis there is a triangular area for attachment of m. interossei. The

similar areas are also located on the bases of spinous processes of the following two thoracic vertebrae.

The spinous processes of the next seven vertebrae (third-ninth) in *Rattus* are almost equal on their height but approximately on one third lower than that of the second thoracic vertebra. The spinous process of the third vertebra is most thin with the pointed tip. The spinous processes of the following six vertebrae are gradually expanded in upper part and thickened in overall length (Tab. 2). In their transverse section these processes look like the very high triangles with narrow basis as their caudal side is more widened than cranial one. Meanwhile, these processes deviate gradually backward from the vertebra vertical axis (up to the sixth thoracic vertebra), extending more and more beyond the caudal margin of the vertebral centra. On the anterior border of the spinous processes of fourth-(seventh) eighth thoracic vertebrae a small flexure is noticeable, that result in the deviation degree of their bases is somewhat larger than their tips. The upper part of the spinous process of tenth thoracic vertebra (vertebra anticlinalis) is nearly vertically directed. In the way the changing of the spinous processes direction is performed, and the processes of the last three vertebrae are already deviate somewhat anteriorly. On the latter there are specific pair crests, starting at a sharp angle from the bases of the spinous processes and extending posteriorly and laterally. Further their increase in caudal direction is noted, and on the last (13-th) thoracic vertebra these crests are most developed.

In *Spalax*, *Nannospalax*, and *Myospalax* the height of spinous process of the second thoracic vertebra is significantly (4–6 times) greater than that of the first vertebra. However, in contrast the condition of *Rattus*, its structure, size and direction do not differ practically from those of the following vertebrae processes. Further the caudal inclination extent of the spinous processes increases gradually up to 10-th (in *Nannospalax*) or 11-th (in *Spalax* and *Myospalax*) thoracic vertebrae which are anticlinal. In this case the spinous pro-

cesses can be practically superposed on one another. The latter in *Myospalax* on the second–ninth thoracic vertebrae are firmly planted in the special triangular concaves, locating at the bases of the following vertebrae. Meanwhile, as a consequence of the some ventro-caudal curvature, the pointed tips of the spinous processes of the second–third thoracic vertebrae are planted also into the upper caudal parts of the following vertebrae processes, where grooves are noted too. The rigidity in this vertebral section increases apparently during the extensible spine movements.

In *Myospalax* the characteristic widening of the spines tips on the third–fourth and eighth–tenth thoracic vertebrae are also observed that seems to be connected with the insertion of the special ligaments here. The latter promotes also the increasing of rigidity in the posterior thoracic section. In all forms mentioned above the gradual thickening of the spinous processes tips takes place, starting from the seventh–ninth thoracic vertebrae. On the last two–three vertebrae the base of the spinous processes is widened considerably, stronger than in *Rattus*, and extending on the overall width of the neural arch. At the same time the spines height is similar with that of the anticlinal vertebra. On the last two vertebrae the spinous processes are similarly directed — vertically upward. In contrast to that of *Rattus*, the caudal crests in the spines bases of the last thoracic vertebrae are absent.

In *Talpa* the spinous process of the first thoracic vertebra is practically absent and those of the following vertebrae are strongly reduced, elongating slightly on the eighth–tenth thoracic vertebrae only, the caudal component being predominated in their direction. The 11-th thoracic vertebra is generally anticlinal. The spinous processes of the last three thoracic vertebrae (particularly of the 11–12-th) are expanded greatly and become higher. Their bases are displaced on the anterior parts of the neural arches. On the last two vertebrae the tips of the spinous processes are considerably widened and thickened and their direction changes to dorso-cranial.

Muscles

Before the immediate description of the cervical muscles it is necessary to clarify the terminology of the crests in the occipital region of skull. The term “occipital crest” (crista occipitalis) in the human anatomy refers to the crest passing onto the sagittal line nearly from the upper margin of the os occipitale up to the foramen magnum (Sinelnikov, 1972). In the veterinary anatomy this term refers to the transverse crest on the boundary of the os occipitale with os interparietale and sometimes also with os parietale (Klimov, 1955), while the sagittal crest is named the protuberancia occipitalis (Nozdachev, 1973). However, in the International Veterinary Nomenclature the term crista occipitalis as in the human anatomy means the sagittal crest (Shaller, 1992). In this connection we recreate the term “crista

lambdoidalis”, which is not used in the International Veterinary Nomenclature. This crest is situated on the boundary of the os occipitale with os interparietale and os parietale further passing along the boundary or immediately on the os temporale itself (Figs. 4–6). If this crest is weakly developed, the muscles are fastened along the boundary of the bones mentioned above. However, in that case we also will describe the muscles attachment on the crista lambdoidalis although it is weakly noticeable.

Among the muscles functioning in the process of throwing the soil outside in burrowers, except the axial cervical muscles, there is series of the shoulder girdle and forelimb muscles.

Muscles of the shoulder girdle involving in the head lifting

M. clavotrapezius in *Rattus* originates from the temporal part of the crista lambdoidalis and is inserted on the middle region of the anterior edge of the scapula. In *Spalax* the origin of this muscle extends by a narrow aponeurosis on the border of the occipital and temporal parts of the crista lambdoidalis to insert by an aponeurosis on the thoracic third of the clavicle, more laterally than m. cleidomastoideus. In *Myospalax* the origin is widened and extends on the crista lambdoidalis from the border with the os interparietale almost up to the pr. mastoideus. It terminates on the thoracic third of the clavicle, more cranially than m. cleidomastoideus. In *Talpa* this muscle is divided into two parts, p. manubrialis and p. clavicularis. Both originate altogether along the crista lambdoidalis passing along the border of the os parietale and bulla tympani. The lateral half of this origin extends up to the tubercle on the bulla tympani (homologue of pr. mastoideus) and is inserted on the anterior margin of the manubrium sterni, being fused with the termination of m. steromastoideus. The medial part (p. clavicularis) of the muscle terminates on the medioventral extremity of the clavicular crest in the region of its articulation with the manubrium sterni.

M. acromiotrapezius in *Rattus*, *Spalax*, and *Myospalax* arises on the midline of the neck from the occiput and up to the spinous process of the second thoracic vertebra (*Rattus*) or the level of the last cervical vertebra (*Spalax* and *Myospalax*). In all three species the termination of this muscle extends from the tuber spinae scapula up to the clavicular extremity of the pr. acromialis and in *Rattus* it passes also on the scapular extremity of the clavicle. In *Talpa* this muscle is reduced.

M. spinotrapezius originates from the spinous processes of the fourth thoracic vertebra — third lumbar vertebra in *Rattus* or fourth–sixth thoracic vertebra — third–fourth lumbar vertebra in *Spalax* and *Myospalax* and from the midline of the back between the second–third lumbar vertebra and the spinous process of the third thoracic vertebra, and also from the fascia lumbalis at the level of the articular processes of the third

lumbar vertebra in *Talpa*. In all forms investigated it is inserted on the tuber spinae scapula. The latter in *Talpa* looks like the triangular prominence with pointed tip. In this connection the termination of the muscle becomes spot like.

M. sternocleidomastoideus in *Rattus*, *Spalax*, and *Myospalax* arises from the pr. mastoideus where m. sternomastoideus is more superficial than m. cleidomastoideus. The latter is inserted in *Rattus* on the middle third of the dorsal edge, in *Spalax* on the thoracic quarter, and in *Myospalax* on the thoracic half of the clavicle. M. sternomastoideus in all three forms terminates on the anterior edge of the manubrium sterni. In *Talpa* this muscle originates by a tendon on the bulla tympani, immediately deeper than m. clavotrapezius p. manubrialis. It fuses with the latter in its termination on the anterior edge of the manubrium sterni. M. cleidomastoideus in *Talpa* takes origin as a small appendix of the m. sternomastoideus tendon and is inserted on the anterior edge of the clavicle, immediately near the termination of the ligamentum acromioclavicularis.

M. rhomboideus capitis in *Rattus* arises from the temporal part of the crista lambdoidalis up to the pr. mastoideus to insert on the dorsal third of the spinae scapulae passing on the cranial half of the lateral surface of the scapula vertebral edge. In *Spalax* and *Myospalax* it divides into the dorsal and ventral parts which differ slightly of bundles direction and power. The first of them in *Myospalax* originates from the overall occipital part of the crista lambdoidalis, and is somewhat displaced from its sagittal part in *Spalax*. Meanwhile, the ventral part extends on the overall temporal part of the crest. The dorsal part in *Spalax* is inserted on a half of the anterior edge of the scapula and on the one tenth part of the fossa infraspinata and in *Myospalax* on the third of the anterior edge of the scapula and on the quarter of the fossa infraspinata. The ventral part terminates on the spinae scapulae up to the pr. acromialis. In *Talpa* the muscle originates on the crista lambdoidalis almost from its sagittal extremity along the specific crest crossing the os interparietale, and from the caudal process of the os parietale up to the tubercle on the bullae tympani. It terminates deeper than m. rhomboideus cervicis on the dorsal part of the scapula, higher than the tuber spinae scapulae and on the vertebral edge of the fossa infraspinata.

M. rhomboideus cervicis and thoracis in *Rattus*, *Spalax*, and *Myospalax* are practically a single muscle originating on the neck midline from the axis level up to the spinous process of the second thoracic vertebra (*Rattus*) or to the last cervical vertebra (*Spalax*, *Myospalax*). It is inserted on the medial surface of the scapular vertebral edge (*Rattus*) or on the medial and lateral surfaces of the cranial half of the scapular vertebral edge (*Spalax*, *Myospalax*).

In *Talpa* m. rhomboideus cervicis by accretion of its right and left sides forms the vertical lamina, the caudo-dorsal edge of which transforms in the transverse ligament uniting the scapulas tips. The muscle fibres passing from the rest part of the lamina terminate on the

cranial half of medial surface of the scapular vertebral edge where the transverse ligament is approximately located at the spinae scapulae level. The termination extends also on the widened surface of the lateral edge of the fossa infraspinata where it covers the termination of m. rhomboideus capitis. M. rhomboideus thoracis in *Talpa* arises on the spinous process of the fourth thoracic vertebra and on the caudal edge of the vertical lamina to insert on the ventral edge of the ligamentum transversarium.

M. serratus ventralis originates from the tips of the pleurapophyses of the last six cervical vertebrae and seven–eight ribs: from the first rib — along its caudal edge and from the remaining ribs — more dorsally than rib cartilages (*Rattus*, *Spalax*, and *Myospalax*). In *Talpa* it differentiates into three parts: cervical and two thoracic. The first arises from the pleurapophyses of the six cervical vertebrae and from the tubercle of the first rib. The dorsal thoracic part originates immediately more ventrally than m. iliocostalis, on the third–fourth ribs (on the one tenth of their length); the ventral thoracic part — on the third–ninth ribs, approximately from the region of their articulation with the rib cartilages. The muscle is inserted on the medial surface of the scapular vertebral edge (*Rattus* and *Talpa*) or on the medial and lateral surface of the infraspinata part of the scapular vertebral edge (*Spalax* and *Myospalax*).

M. pectoralis superficialis in *Rattus* arises on the overall sternum: from the cranial edge of its manubrium up to the caudal widening of the pr. xiphoideus; it is inserted on the distal part of the crista tuberculi majoris. In *Spalax* it originates at somewhat anterior to the manubrium sterni and extends up to the widening of the pr. xiphoideus and also from the fourth–eighth rib cartilages occupying on their lateral surface: 5% — on the fourth, 40% — on the fifth, 60% — on the sixth, 20% — on the seventh, and 5% — on the eighth. In *Myospalax* the differentiation into two parts is projected. P. externa arises from the manubrium sterni up to the pr. xiphoideus and from the lateral surface of the second–seventh rib cartilages occupying: 15% — on the second and third, 75% — on the fourth, 50% — on the fifth–sixth, and 30% — on the seventh. It terminates on the lateral and medial surfaces of the distal third of the crista tuberculi majoris enclosing the m. clavodeltoideus termination on the lateral side. P. interna originates deeper than m. pectoralis profundus onto the caudal edge of the second–third ribs, more dorsal than their cartilages to insert from the apex of the crista tuberculi majoris up to its proximal extremity.

In *Talpa* it differentiated into p. praesternalis and p. sternalis. The first arises through the accretion of the right and left sides in front of the manubrium sterni, the length of this accretion region being approximately equal to the third of the crista tuberculi majoris length. It terminates on the crest which extends from the crista tuberculi minoris, more proximally than the opening for m. biceps brachii, up to the crista tuberculi majoris. P. sternalis originates from the tubercle of the manubrium sterni, in front of which one of the m. subclavius parts

arises. Its origin extends also along the whole sternum up to the widening of the pr. xiphoideus and on the bases of the second–seventh rib cartilages occupying on their surfaces: 8% — on the second, 31% — on the third, 42% — on the fourth, 40% — on the fifth, 52% — on the sixth, 7% — on the seventh. Meanwhile, from the second–third rib cartilages up to their articulation with ribs the independent p. interna takes origin. All these parts fuse in terminal aponeurosis which is inserted on the crista tuberculi minoris, more proximally than the opening for m. biceps brachii. Thus, in *Rattus*, *Spalax*, and *Myospalax* this muscle terminates on the crista tuberculi majoris, while in *Talpa* it terminates on the crista tuberculi minoris.

M. pectoralis profundus in *Rattus* springs from the first four segments of the sternum and terminates on the crista tuberculi majoris passing from the latter onto the tuberculum minoris and pr. coracoideus. In *Spalax* it takes origin from the lateral surfaces of the second–fifth rib cartilages starting from the preceding muscle attachment up to their border with ribs; it is inserted on the pr. coracoideus of the scapula. In *Myospalax* it arises on the first three ribs occupying all the lateral surface of the first rib and up to the second–third rib cartilages; it is inserted on the pr. coracoideus only. In *Talpa* it originates from the lateral crest of the manubrium sterni between the attachments of the first and second rib cartilages to insert on the pr. coracoideus.

M. subclavius in *Rattus* starts from the distal part of the first rib and terminates on the middle part of the caudoventral surface of the clavicle. In *Spalax* it takes origin from the cranial edge of the first rib on the border with its cartilage; it is inserted on the scapular extremity of the clavicle (one fourth of its length), on the lateral side and also on its medial side (a half of length), passing from the clavicle onto the caudal edge of the pr. acromialis. In *Myospalax* it arises from the approximately whole craniolateral surface of the widened first rib and terminates on the scapular extremity of the clavicle (two thirds of its length) on the lateromedial side passing from it onto the anterior edge of the pr. acromialis and the ventral part of the spinae scapulae.

In *Talpa* it differentiates into three portions which originate from the sternum part of the first rib cartilage and from the manubrium sterni. P. scapularis arises from the base of the first rib cartilage and crista lateralis of the manubrium sterni; p. clavicula interna — on the same crest but more laterally than p. scapularis; p. clavicula externa apart from the crest occupies the overall lateral surface of the manubrium sterni part which is before ribs situated. Their terminations are the following: p. scapularis — on the acromial half of the lig. acromioclavicularis passing from it onto the pr. acromialis and one sixth part of the spinae scapulae length; p. clavicula interna — near the lig. acromioclavicularis on the internal surface of the clavicle; p. clavicula externa — on the cranial process of the clavicle and on its crest, near the joint with the sternum.

Axial muscles involving in the head lifting

M. splenius in *Rattus* originates from the lateral edge of the triangular lamina locating on the tip of the spinous process of the second thoracic vertebra, and from the neck midline up to the level of the axis crest to insert on the temporal part of the crista lambdoidalis. In *Spalax* and *Myospalax* it arises from the neck midline where the accretion of the right and left muscle sides forms the connective-tissue lamina extending up to the spinous processes of the second–third thoracic vertebrae. In both species the muscle origin extends up to the level of the last cervical vertebra without connection with its spinous process. Cranially its insertion extends on the 20% of neck length in *Myospalax* and on the 12% in *Spalax*. It terminates along the crista lambdoidalis near the sagittal line extending up to the pr. mastoideus (in *Spalax*) or onto the temporal part of this crest do not reaching the pr. mastoideus (in *Myospalax*). In *Talpa* this muscle takes origin from the lig. transversus uniting the tops of both scapulas and from the caudal three fourths of the neck midline; it is fastened on the lateral half of the crest which is situated between the acoustic foramen and pr. mastoideus.

M. semispinalis capitis in *Rattus* arises by its superficial part from the metapophyses of the fourth–seventh thoracic vertebrae and by its deep part from the postzygapophyses of the third cervical vertebra up to the metapophyses of the fourth thoracic vertebra. Further, these parts fuse and terminate altogether on the overall occipital part of the crista lambdoidalis starting from the sagittal line. In *Spalax* and *Myospalax* the superficial part of the muscle originates from the metapophyses of the fourth–seventh thoracic vertebrae having the pedicles from the second–seventh costal tubercle. The deep part in this case takes origin from the postzygapophyses of the third cervical vertebra up to the metapophyses of the fourth thoracic vertebra. Both parts fuse and terminate on the overall occipital part of the crista lambdoidalis. In *Talpa* it differentiates into two parts, the cranial part arises by a thin aponeurosis from the postzygapophyses of the third–fifth cervical vertebrae and caudal part arises from postzygapophyses of the seventh cervical up to the metapophyses of the third thoracic vertebrae. The muscle is fastened on the occipital part of the crista lambdoidalis.

M. semispinalis cervicis in *Rattus* originates from the neural arches of the third cervical up to the first thoracic vertebrae and from the metapophyses of the second–seventh thoracic vertebrae. It is inserted on the caudal edge of axis and on the spinous processes of the cervical vertebrae. In *Spalax* and *Myospalax* it arises by tendon pedicles from the dorsal arches of the sixth–seventh cervicals and metapophyses of the first two thoracic vertebrae and also by the muscular pedicles from the metapophyses of the third–fourth thoracic vertebrae. It terminates on the caudal edge of the axis crest extending up to the extremities of its pleurapophyses. In *Talpa* it takes origin by three muscular pedicles

from the metapophyses of the first three thoracic vertebrae and postzygapophyses of the last three cervical vertebrae. It is inserted on the spinous processes of third-fourth cervical vertebrae and caudal surface of the axis crest.

M. longissimus capitis in *Rattus*, *Spalax*, and *Myospalax* arises from the metapophyses of the first three thoracic vertebrae and from the postzygapophyses of the last four cervical vertebrae; it terminates on the temporal part of the crista lambdoidalis, somewhat more caudally than the pr. mastoideus. In *Talpa* this muscle originates from the pleurapophyses of the third-fifth cervical vertebrae only and is inserted on the lateral part of the crest between the acoustic foramen and pr. mastoideus.

M. longissimus cervicis in *Rattus*, *Spalax*, and *Myospalax* takes origin from the neural arches of the third cervical – fourth thoracic vertebrae and terminates on the pleurapophyses of all cervical vertebrae. In *Talpa* it arises from the neural arches of the second-fourth thoracic vertebrae and is fastened on the pleurapophyses of the last three cervical vertebrae.

M. rectus capitis dorsalis major in all forms investigated springs from the dorsal part of the lateral surface of the axis crest and passes to the middle part of the crista lambdoidalis p. occipitalis. Its lateroventral bundles are often designated as m. rectus capitis dorsalis medius.

M. rectus capitis dorsalis minor in *Rattus*, *Spalax*, and *Myospalax* originates from the atlas dorsal arch and terminates on the caudal surface of the os occipitale, immediately more ventrally than the preceding muscle. In *Talpa* it arises from the tuberculum on dorsal arch of atlas and at the termination it fuses with the terminal tendon of the preceding muscle.

M. obliquus capitis caudalis in all forms investigated takes origin from the lateral surface of the axis dorsal arch and is inserted on the caudal edge of the atlas wings.

M. obliquus capitis cranialis in all forms investigated arises from the dorsal surface of the atlas wings and is inserted laterally from the dorsal edge of the termination of m. rectus capitis dorsalis major on the crista lambdoidalis p. occipitalis.

M. rectus capitis lateralis in *Rattus* starts from the cranial edge of the atlas wings and terminates from the level of the pr. mastoideus extending more ventrally on the pr. jugulares. In *Spalax*, *Myospalax*, and *Talpa* it originates from the ventral surface of the atlantal wings and is fastened on the most ventral part of the crista lambdoidalis.

Extensors of the elbow joint

M. triceps brachii has three heads:

M. anconeus longus in *Rattus* originates from the ventral third of the caudal edge of the scapula; in *Spalax* not only from the overall caudal edge of the scapula but from its caudal crest also and from the

region between them; in *Myospalax* not only from the overall caudal edge of scapula but from the ventral two thirds of the spinae scapulae; in *Talpa* from the ventral third of the caudal edge of the scapula. In all forms it terminates on the olecranon apex.

M. anconeus lateralis in *Rattus* takes the origin by the tendon from the dorsal surface of the crista tuberculi majoris. In *Spalax* and *Myospalax* the initial tendon extends from the humeral neck up to the distal end of the crista tuberculi majoris. It is inserted on the olecranon apex, more laterally than the termination of m. anconeus longus. In *Talpa* the muscle differentiates into two parts, the first of which springs from the distal part of the lateral surface of the crista tuberculi majoris and the second part from the dorsal surface of the crista epicondylis lateralis. The both terminate on the top of the olecranon lateral tuberculum.

M. anconeus medialis in *Rattus*, *Spalax*, and *Myospalax* arises from the medial side of the proximal third of the humerus dorsal surface. On the lateral part of this surface it is replaced by the m. brachialis origin. More distally the m. anconeus medialis origin becomes wider and occupies the overall dorsal surface of the humerus passing on the epicondylar surface. On the surface of the lateral epicondyle it passes onto the origin of m. epitrochleoanconeus. In *Talpa* the muscle differentiates into several independent bundles. One of them originates on the medial tendinous mirror of m. teres major and further passes on the dorsal and ventral surfaces of the distal part of the crista tuberculi minoris; a second bundle takes origin on the dorsal surface of the crista epicondylis medialis; the origin of a third bundle expends more laterally than the termination of m. teres major up to the proximal end of the tuberculum minor; a fourth bundle arises not only more laterally than m. brachialis but more medially than the latter penetrating in lateral concavity. In all forms mentioned above the muscle terminates on the dorsal surface of the olecranon.

M. epitrochleoanconeus lateralis in *Rattus*, *Spalax*, and *Myospalax* originates on the dorsal surface of the lateral epicondyle as immediate continuation of m. anconeus medialis and is inserted on the lateral line of the ulna from the olecranon apex up to the humerus level (*Rattus*) and partly also on the ulna body (*Spalax* and *Myospalax*). In *Talpa* the muscle differentiates into two parts which originate on the dorsal surface of the lateral epicondyle; the proximal part is fastened on the back side of the lateral tuberculum of the olecranon apex and the second part along the lateral crest up to the middle of the ulna.

M. epitrochleoanconeus medialis in *Rattus*, *Spalax*, and *Myospalax* arises from the dorsal surface of the medial epicondyle and terminates on the caudomedial surface of the olecranon apex. In *Talpa* it takes origin from the special concavity of the dorsal surface near the trochlear basis and is inserted on the back surface of the medial tuberculum of the olecranon apex.

M. dorsoepitrochlearis in *Rattus*, *Spalax*, and *Myospalax* originates from the lateral surface of m. latissi-

Table 3. Dynamics of the skeletal elements displacements at pushing the soil forward inside a tunnels (1) and lifting the soil with the head (2) in *Spalax microphthalmus*.

a–d — successive stages of movement cycle (through four frames on fifth) at speed 64 frames per second. A–G — position changes of the skeletal long axes in respect to the horizontal plane (in degrees): A — antibrachium; B — humerus; C — scapula; D — cervical vertebrae; E — sternum; F — dorsal line of skull; G — thoracic vertebrae. H–L — relationship between the different distances (in %) and distance from the os nasale tip up to the os occipitale apex: H — distance between of the nose tip and the vertical line, drawn from the forward point of the manus; I — distance between the scapula top and the upper dorsal point of os occipitale; J — distance between the horizontal plane of the soil and the manubrium sterni; K — distance between the scapula and olecranon tips; L — distance between of the horizontal plane of the soil and the upper dorsal point of the os occipitale.

	A	B	C	D	E	F	G	H	I	J	K	L
1a	10	94	7	86	11	120	38	0	144	12	83	129
1b	22	46	46	46	12	122	28	58	120	14	98	125
1c	29	43	32	44	20	138	18	72	122	17	92	137
1d	47	49	40	34	23	146	12	106	135	24	72	168
2a	36	38	62	5	3	148	51	104	96	29	83	106
2b	47	73	42	27	0	170	41	100	88	37	92	159
2c	44	70	28	68	12	192	22	50	89	52	76	207
2d	49	75	20	74	12	208	22	37	85	56	67	204

mus dorsi in region of its passing into the terminal tendon and is inserted on the olecranon apex extending more distal onto the superficial fascia of the forearm. In *Talpa* the muscle springs on the medial tendinous mirror of m. teres major, and its termination extends from the olecranon apex along the lateral edge of m. flexor carpi ulnaris up to a half of the forearm length.

The functional analysis

The adaptation for throwing the soil out with the head have to cause a such transformation of the musculoskeletal system, when the muscles strength must be sufficient enough for the lifting of the load equal to the soil weight thrown out. The results of the field observations and the special experiments indicate that *Spalax* and *Myospalax* are able to lift a load with the head which surpass 20 times their body weight (Gambaryan, 1960; Gambaryan & Gasc, 1993). *Talpa* can move the soil aside by the forelimbs with an effort more than 2–3 kg, while its body weight is about 68–100 g (Scotzen, 1958; Gambaryan *et al.*, 2002). Moreover, in the process of throwing the earth away in *Talpa* soil columns are observed, their height being 25–30 cm and weight about 2.5–3.0 kg. The analysis of the lifting the load with the head in *Myospalax* showed that in this case the following processes take place: 1) the lifting of the body between the extremities; 2) the extension of the elbow joint; 3) the extension of the occipital joint (Gambaryan & Gasc, 1993). Meanwhile, the extension of the cervicothoracic joint depends probably on the combinations with actions of the occipital joint extensors. In each process mentioned above the exerted force of the muscles has to be more than a load weight, otherwise the load could not be lifted and the soil could not be thrown out of a tunnel.

The cinefluorography of the burrowing activity in *Spalax* permits to consider two processes connected with throwing the soil out of a feeding passage: 1) pushing the substrate forward inside a tunnel (Tab. 3; Fig. 9); 2) lifting the soil with the head and throwing it out on the surface (Tab. 3; Fig. 10). These two processes of the burrowing activity require the most energy consumption.

The first frame of the soil pushing cycle (1) is positional. One can see that *Spalax* moves the hands forward maximally reaching by finger tips the level of the anterior part of the snout (Fig. 9). For this aim the humerus is pushed forward, its long axis being nearly vertical and the caput humeri being on the skull level. Meanwhile, the vertical humerus position leads to the nearly horizontal scapula position (Tab. 3). From this moment the active phase of the soil pushing inside a tunnel originates, when the body rises slightly (up to the 7% to the dorsal length of skull). Through the three fourths of cycle extent the shoulder joint keeps its position on the skull level approximately, and the soil pushing forward occurs owing to the lifting of the forearm with the initial flexion of the shoulder (from 103° up to 76°) and elbow (from 107° up to 68°) joints and their final extension (up to 93° in shoulder and up to 97° in elbow joints). Simultaneously the neck line turns from the nearly vertical into the nearly horizontal position, the dorsal line of the head displaces on the 26° and the occipital joint is extended (from 48° up to 108°) (Tab. 3; Fig. 9).

The series of the cycles analyzed indicates the variety of the thoracic vertebrae positions at the initial phase of the soil pushing forward inside a tunnel. Often in the beginning the hindlimbs were stood closer to the forelimbs. In this case the back was curved and an angle between the longitudinal axis and thoracic vertebrae

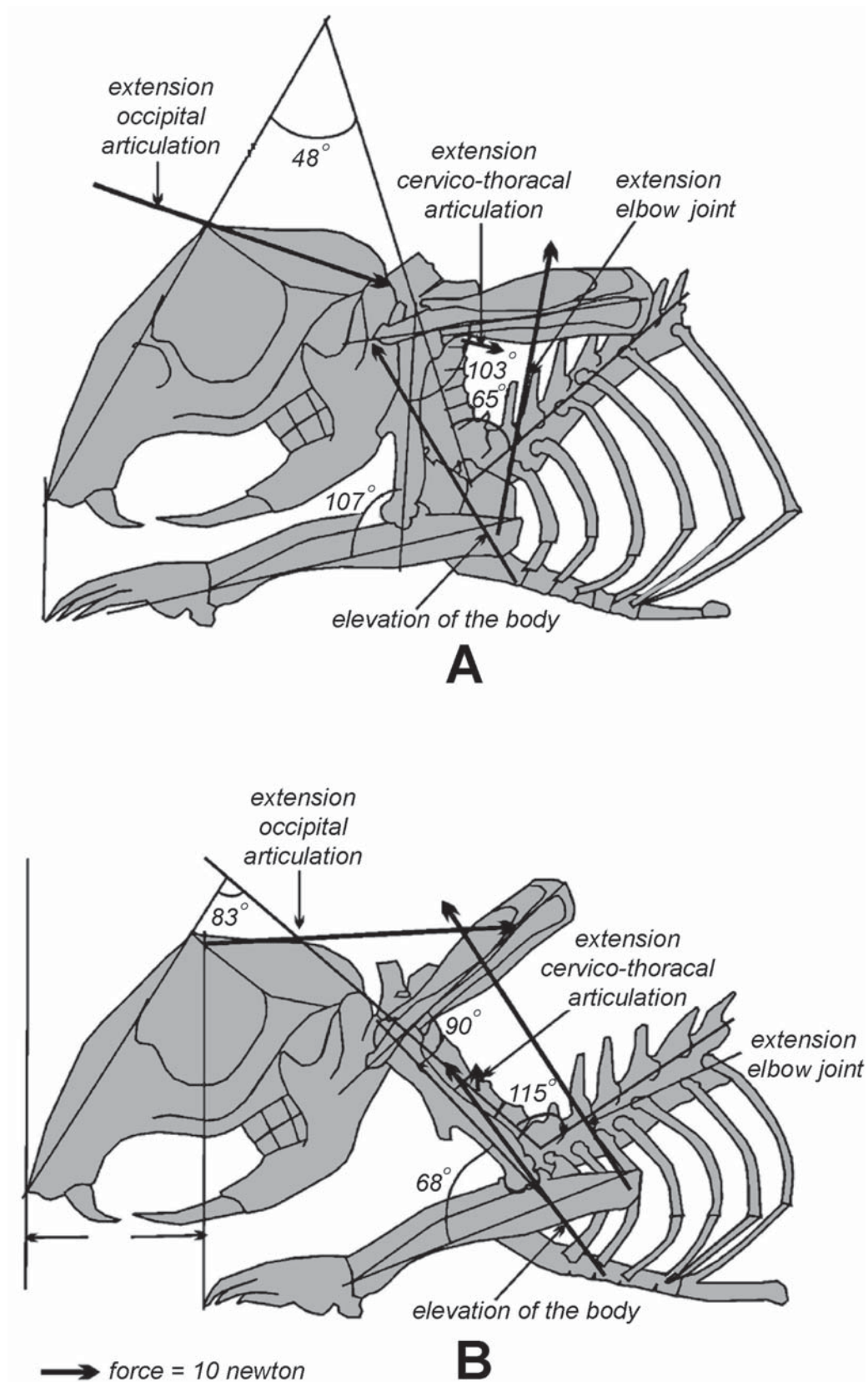


Figure 9. Cinefluorography of movement cycle in the process of pushing the soil forward with the head in *Spalax microphthalmus*.

A–D — several successive positions in lateral view (every fourth frame is pictured; speed of filming 64 frames/sec).

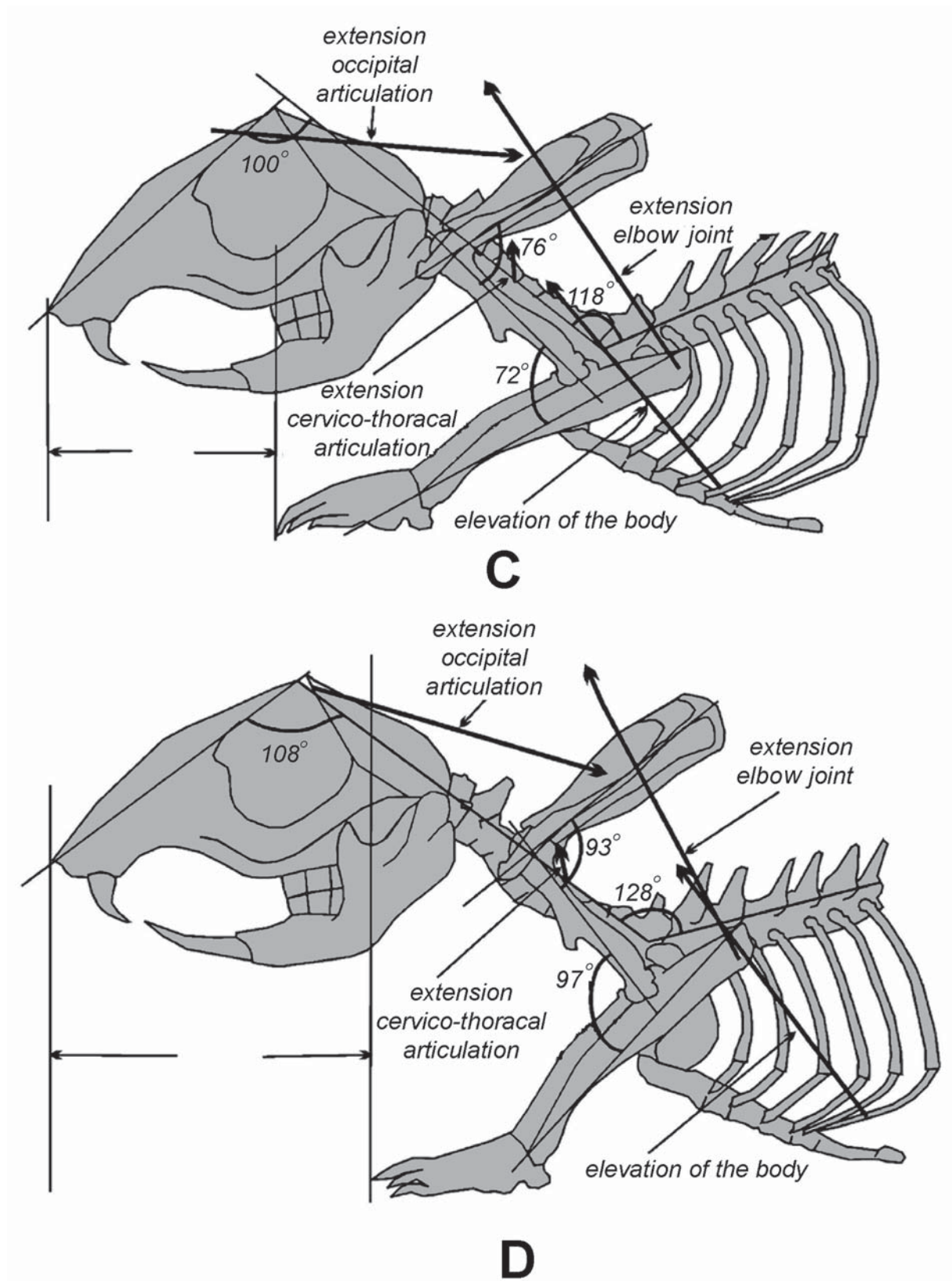


Figure 9 (continued).

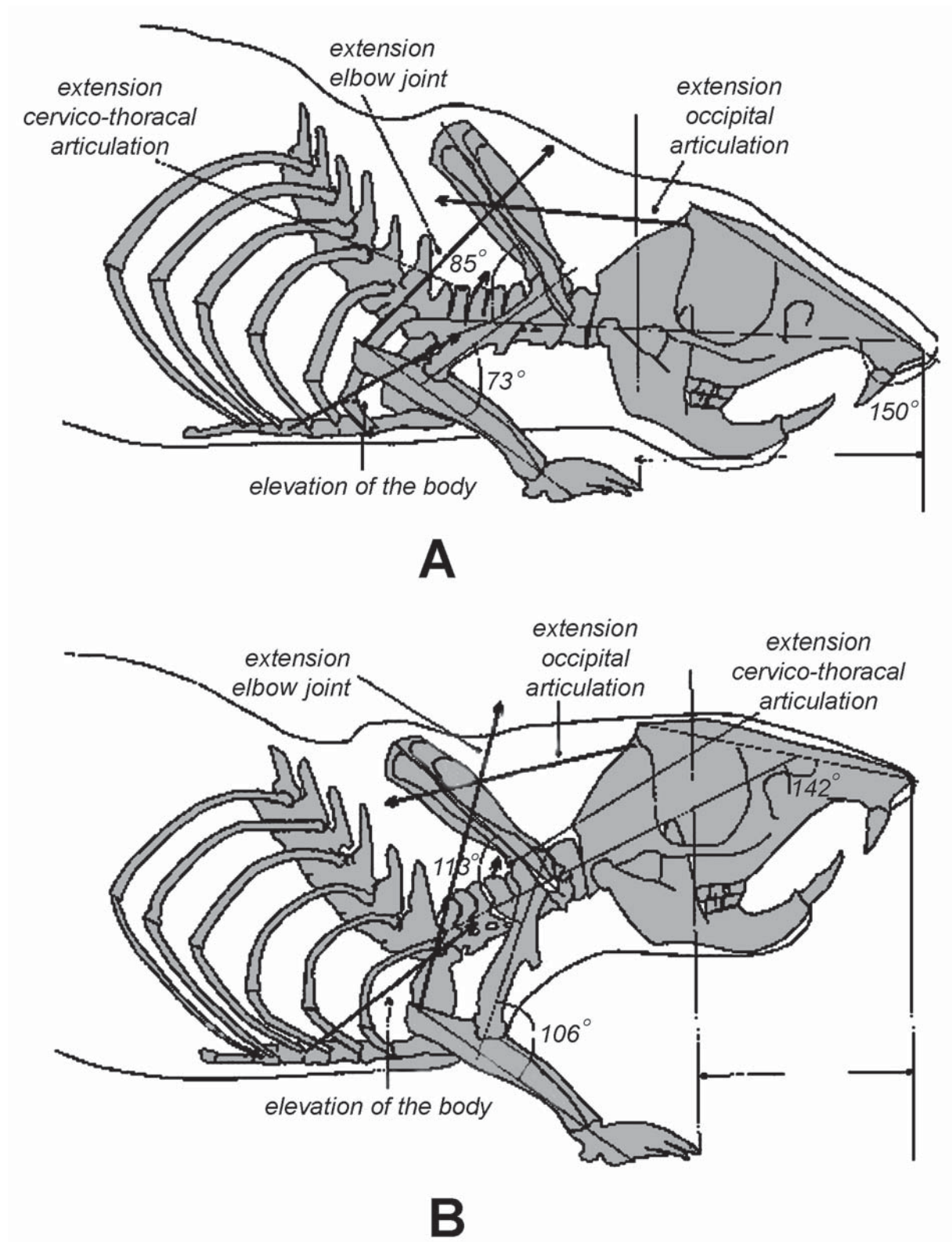


Figure 10. Cinefluorography of movement cycle in the process of lifting the soil with the head in *Spalax microphthalmus*. A–D — several successive positions in lateral view (every fourth frame is pictured; speed of filming 64 frames/sec).

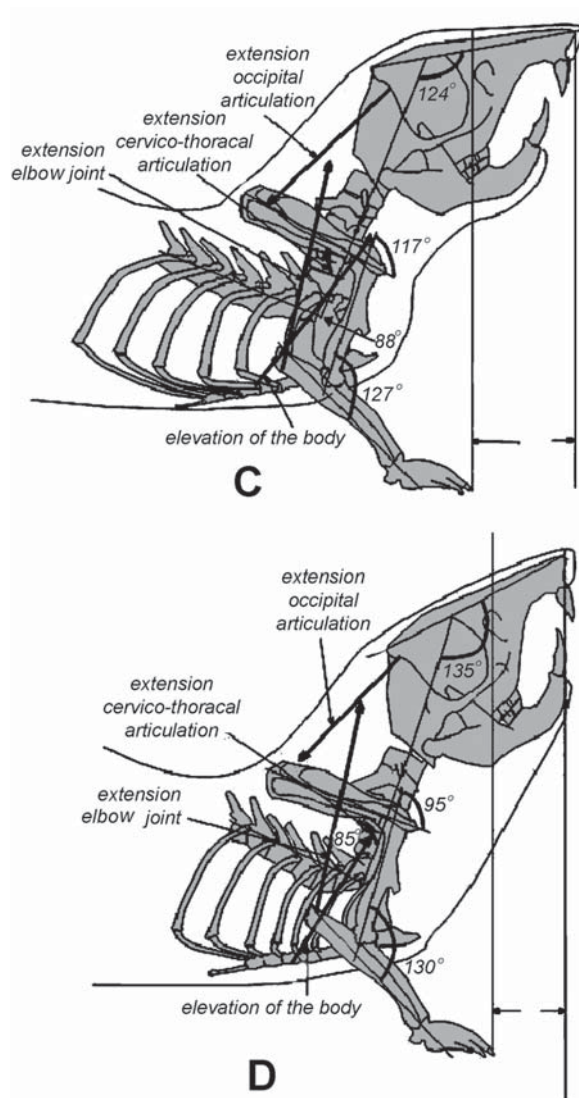


Figure 10 (continued).

line becomes similar approximately to that on the initial frame of the process (2) the soil lifting with the head. The last process originated more standard while the process of the soil pushing forward could start from such moment even, when the foot touched the soil by the back side, that is, it did not take part in the phase of support. In this case the thoracic vertebrae line was still more horizontal than in the cycle chosen for the analysis.

The process of lifting the soil with the head originates almost from the same position, on which the process of pushing the soil forward inside a tunnel terminates. Feet were rather constant stood, thus the thoracic vertebrae line was situated at an angle of 51° to the longitudinal axis (Tab. 3). Further the moving of the sternum forward resulted in the decreasing of this angle up to 22° . During the soil lifting with the head the snout tip transferred backwards, so that the hand was displaced forward. To the end of this process the vertical line drawn from the head center fell in the area of the

hand support. The extension of the occipital joint with the change of the skull dorsal line position was attended by the simultaneous flexion of the cervicothoracic region (from 130° up to 80°). Meanwhile, the neck itself rose arriving to the cycle end the position at an angle of 74° to the longitudinal axis (Fig. 10, Tab. 3). In process of the soil pushing forward, on the contrary, the neck position changed from the nearly vertical (86°) up to the nearly horizontal (34°) (Fig. 9). Whereas at the soil pushing forward the anterior sternum extremity only rose under the soil level (on the 7% relatively to the length of the skull dorsal line), at the soil lifting with the head the body transferred significantly upwards between the extremities (approximately on the 40% to the length of the skull dorsal line) (Figs. 9 and 10; Tab. 3). On Fig. 10C, D one can see, whereas the sternum rises under the soil level, the manubrium sterni is dropped relative to the elbow joint. It testifies that the summary force of the body elevation is not equal to a load, and in the way the cycle of the soil lifting with the head terminates.

To determine the forces, which can be exerted at the soil pushing forward inside a tunnels and its lifting with the head, the vector system was used (Tab. 4). The vector direction was defined by the topography of the muscle origin and termination. The length of the resultant vector is equal to the vectors sum of the forces acting in some region. As a result of all the geometrical constructions on the Figs. 9 and 10 the resultant vectors reflecting the muscle work in three processes are displayed only: 1) the body lifting between the extremities (the summary vector of mm. pectoralis superficialis et profundus, subclavius, and serratus ventralis p. thoracalis); 2) the extension of the elbow joint (the summary vector of mm. anconeus longus, lateralis et medialis, epitrochleoanconeus lateralis et medialis, and dorsoepitrochlearis); 3) the extension of the occipital joint (the summary vector of mm. rhomboideus capitis, splenius, semispinalis capitis, longissimus capitis, rectus capitis dorsalis major et minor, rectus capitis lateralis, and obliquus capitis cranialis) (Tab. 5).

Furthermore, the vectors of the cervicothoracic extensors (mm. semispinalis cervicis, longissimus cervicis, and serratus ventralis p. cervicalis) were summarized too. The peculiarities of their action are practically conditioned by the muscles action in other joints. At the soil pushing through a tunnels the active extension (from 48° up to 108°) of the occipital joint is observed, the latter being possible by support on the cervical vertebrae, when the neck is increasingly pulled forward (Figs. 9 and 10). Accordingly at throwing the soil away the neck rises subsequent to the head. It is interesting to note the difference in the directions correlation of the summary force of the occipital joint extensors at pushing the soil through a tunnels and throwing its out with the head. In the first case the forces resultant vector passes significantly closer to the occipital joint than in the second case. It means the force moment of this joint extension increases noticeably at lifting the soil with the head. In the case of the soil pushing forward the

Table 4. Relative weight and force of some axial and forelimbs muscles.
 A — *Rattus norvegicus*, B — *Nannospalax nehringi*, C — *Myospalax myospalax*, D — *Talpa europaea* (1 — ratio of the muscle weight to the total weight of the fore and hind limbs muscles, in %; 2 — force of the muscle, in N).
 Abbreviations: cerv. — cervicis, thor. — thoracis, superfic. — superficialis.

Muscle	A ₁	A ₂	B ₁	B ₂	C ₁	C ₂	D ₁	D ₂
clavotrapezius	0.6	0.6	0.05	0.2	0.6	1.2	1.1	0.6
acromiotrapezius	1.1	1.9	1.9	4.2	0.8	1.4	—	—
spinotrapezius	1.0	0.7	5.0	4.9	1.7	2.6	1.0	0.2
rhomboideus cerv.+ thor.	0.9	1.4	2.3	9.3	2.3	9.5	1.3	0.8
rhomboideus capitis	0.6	0.5	8.3	21.5	6.5	18.6	1.4	0.3
latissimus dorsi	3.4	3.8	7.3	11.4	6.5	11.7	8.3	2.3
sterno-mastoideus	0.8	1.0	1.4	3.3	0.7	1.7	0.6	0.3
cleido-mastoideus	0.1	0.4	0.6	2.3	0.5	1.3	1.1	0.1
pectoralis superfic.	4.6	2.8	7.3	19.7	13.0	36.6	15.3	14.4
pectoralis profundus	1.3	2.0	1.6	2.9	2.6	10.1	0.6	1.5
subclavius	0.2	0.2	3.5	12.7	1.3	8.9	1.7	4.0
serratus ventralis	3.3	5.1	4.7	9.8	3.1	8.5	3.6	2.6
atlantoscaphularis	0.1	0.3	0.2	0.8	1.5	2.9	—	—
anconeus longus	3.5	9.1	8.2	40.7	9.5	32.7	3.7	2.5
anconeus lateralis	0.9	2.5	1.9	8.0	2.6	11.1	1.7	2.0
anconeus medialis	0.8	2.0	1.9	7.9	1.7	9.9	2.6	3.5
dorsoepitrochlearis	0.2	0.3	1.9	6.3	1.6	7.9	0.2	0.2
epitrochleoanconeus	0.05	0.4	0.1	1.1	0.2	2.0	1.2	2.1
splenius	1.3	2.6	4.0	10.2	2.3	12.3	2.9	0.7
semispinalis capitis	2.6	2.7	7.3	16.1	5.1	15.9	1.2	0.6
semispinalis cervicis	0.8	1.4	1.7	3.2	0.7	5.2	0.3	0.2
rectus capitis dorsalis major	0.7	1.1	2.3	3.5	2.5	7.9	0.4	0.2
rectus capitis dorsalis minor	0.1	0.5	0.8	3.7			0.3	0.3
rectus capitis lateralis	0.1	0.3	0.8	2.3	0.8	0.4	—	—
obliquus capitis caudalis	0.3	1.3	0.3	1.2	0.2	1.9	0.1	0.3
obliquus capitis cranialis	0.1	0.6	0.3	1.5	0.6	4.1	0.05	0.1
longissimus capitis	0.3	0.7	0.4	1.2	0.2	1.1	0.3	0.3
longissimus cervicis	0.3	0.6	0.3	1.0	0.1	0.1	0.1	0.1
Forelimb muscles weight relative to total weight of forelimb and hindlimb muscles, %	36.3	—	69.7	—	72.9	—	83.2	—

value of the force application lever (relatively to the length of the skull dorsal line) changes from 8% up to 25% and at the lifting the soil with the head it exceeds 40% on all the frames. As a result the increasing of the pressing force of the head on the soil is defined not only by the extensors action, but at the increasing of the force application lever as well.

Accordingly to the working stages in these two most power-consuming processes the definite changes of the summary forces and directions of their action take place. So, during pushing of the soil through a tunnel, the application point of the summary force of body eleva-

Table 5. Relative weight (%) and force (N) of the main muscles groups.

Taxon	Occipital joint extensors		Elbow joint extensors		Muscles lifting the body	
	%	N	%	N	%	N
<i>Rattus</i>	4.7	8	5.4	16.9	9.4	9.2
<i>Spalax</i>	17.4	50.7	17.1	64.0	17.4	45.9
<i>Myospalax</i>	20	45.6	20	69.6	18.2	67.0
<i>Talpa</i>	3.5	2.2	9.4	10.3	21.2	22.5

tors shifts backwards. While in the beginning of this process the application point is situated in the manubrium sterni region, to its end it is of approximately on a half of length of the seventh rib cartilage (Fig. 9A, C). As a result its longitudinal component increases, whereas an angle of the force direction to the horizontal plane does not change almost. The lever of the force application is the value of the perpendicular, drawn from the rotation point in the cervicothoracic joint to the action line of the summary force lifting the body between the forelimbs. In this case its length in the beginning of the process will be consist 17% of the skull dorsal line length decreasing up to 8% on the second frame, up to 0% on the third frame and up to 40% on the last frame (Fig. 9A–D). During the lifting the soil with the head the point of force application shifts rather forward, and an angle between the vector direction of summary force of the body elevators and the horizontal plane increases noticeably.

The work of the elbow joint extensors is one of the important links at the soil pushing through a tunnels and its lifting with the head. In the first case the vector of their summary force in the beginning is almost vertically directed with some caudal inclination (100°) (Fig. 9A). Further its direction changes sharply to obtain strongly cranial slope, and then an angle of vector inclination to the horizontal line increases again, from 58° up to 64° (Fig. 9B, C, D). In the second case, during the lifting the soil with the head an angle of inclination of the summary force vector increases progressively, from 46° to 78° (Fig. 10A, D).

For the extension of the occipital joint apart from its extensors forces, the summary force of the body elevators opposite directed is of a great importance. The pressure of both these forces influences on the cervical vertebrae structure which are accreted often in *Spalax* and *Myospalax*. In the latter axis with third–fourth cervical vertebrae is accreted and they act as a single whole. Meanwhile, the lifting of the neck is executed in joints of the first thoracic vertebrae. In this region the influence of a two opposite factors takes place. On the one hand, for the lifting of the neck the rigidity of support is necessary, on another hand, the latter means the minimum mobility. During the digging the burrowers have to turn around on 180° inside a tunnel, since they throw the soil out through a special passage. The latter have to be narrower for the economy of the burrowing process but for the convenience of turns a wide tunnels are more profitable. *Myospalax* looses the soil by the claws which are powerful and long, so that the limbs protrude beyond the whole skin-muscle sack of the body more significantly than those in spalacids. As a result the width of a tunnel in respect to the body diameter in *Myospalax* is approximately 1.5 times more than such in spalacids. Therefore *Myospalax* can turn around in a tunnel more easily than *Spalax*. As a result the withers in *Myospalax* are harder than in spalacids, in which the greater mobility in this region is still required.

The necessity of the rigid base for the neck support at the lifting of the head in both groups resulted in

similar changes in the first segment of the thorax. Thus, the powerful manubrium sterni is developed and the rib cartilage of the strongly widened first rib is adherent to it. The rib tuberculum of the latter is also widened and has the attachment on the wide articular surface of the diapophysis of the first thoracic vertebra. Meanwhile, in *Spalax* the first rib tuberculum is more convex and symmetrical than such in *Myospalax*. As a result the mobility extent at the articulation with diapophysis of the first thoracic vertebra in *Myospalax* is noticeably less than one in *Spalax*. Moreover, in both forms, in contrast to *Rattus*, the pleurapophysis of the seventh cervical vertebra does not take part in the attachment of the first rib tuberculum. However, in *Myospalax* the latter connects by ligament with the pleurapophysis tip, which approaches closely to the diapophysis extremity of first thoracic vertebra but has not its own articular facet. This ligament restricts also the mobility at the articulation. In the way, in *Myospalax* the rigidity of the cervicothoracic joint increases and the whole vertical mobility of the neck, in contrast to such of *Rattus* and *Spalax*, are mainly observed between the first-second thoracic vertebrae. Moreover, in spalacids and *Myospalax* the system of the significantly elongated spinous processes of the first thoracic vertebrae forms the specific withers — the organ of the vertebral column rigidity (Brovar, 1935, 1940). In *Myospalax* the spine tips of the 3–6-th thoracic vertebrae are widened greatly for the over spine ligament insertion, which increases the rigidity of this region also. The real withers occur in ungulates, the spine tips of which are widened and joined through the over spine ligament. In carnivores the elongated spinous processes are also in the forward part of the thorax, but the over spine ligament is absent. Thus, the withers rigidity is relative and the vertical mobility in this region decreases a little. In the way, the withers of spalacids are more similar to such of carnivores, while the withers of *Myospalax* are similar to such of ungulates.

The main changes of musculature can be estimated by means of the relative weight of the muscles working in the joint links mentioned above (Tab. 4, 5). These data indicate that in *Rattus* the occipital joint extensors are about five–six times and in *Talpa* 21–23 times weaker than those in *Spalax* and *Myospalax*. The elbow joint extensors in *Rattus* are about four times and in *Talpa* six–seven times weaker than those in *Spalax* and *Myospalax*. The relative weight of muscles lifting the body between the forelimbs in *Rattus* are less nearly by half than such in burrowers throwing the soil out with the head. It seems to be connected with in *Rattus* the main work of the skeleton and muscles is involved by the adaptation to the jumping pattern of the movement. During the landing phase on the forelimbs the shoulder and elbow joints bend sharply, the body is dropped between the forelimbs and the head is dropped too. At this moment the extensors of the shoulder and elbow joints, the elevators of the head and neck and the muscles counteracting the body dropping work in the yielding regime cushioning a shocks (Kuznetsov, 1999).

Whereas in *Spalax* and *Myospalax* at throwing the soil out with the head the forces which are about 20–30 times more than their own weight must be developed, in *Rattus* so great efforts are not required for the counteraction the body pushes.

In *Talpa* the relative weight of muscles group lifting the body between the limbs is more even than such in *Spalax* and *Myospalax* (Tab. 5). It seems to be related with the specific mode of burrowing when the soil is pushed apart with the forelimbs in perpendicular to the sagittal plane direction (Reed, 1951; Gambaryan *et al.*, 2002). *M. pectoralis superficialis* is one of the main muscles providing this motion, and its relative weight in *Talpa* is most of those of other forms investigated (Tab. 4). In process of burrowing in *Talpa* the snout tip is always situated behind the claws tips (Gambaryan *et al.*, 2002). To confine this position the neck curve takes place, so that it arch like becomes and atlas displaces on the ventral part of the occipital condyles. During the catching and feeding of prey only the neck in *Talpa* is straightened and the snout tip at the front of forelimbs is found.

In Todorova (1927) and Boker (1935) the mode of burrowing of *Talpa* is named “swimgraben”, since they consider its movements during both the burrowing and swimming to be similar. The analysis of the cinefluorography of the digging activity in *Talpa* indicates there are essential distinctions between the types of its movement during the burrowing and swimming activity. At swimming the body motions are zigzag and most important. Owing to these movements only the wide hands of *Talpa* can throw the water out at an angle backwards making possible a swimming effect. At burrowing both forelimbs move laterally, this motion being symmetrical under conditions of similar soil solidity from the both sides. However, if the soil is more loose from one side, the hand of *Talpa* will move more rapidly there than in more solid region and will be farther remove from the body. In this case the side curves of the body are practically absent (Gambaryan *et al.*, 2002).

As cinefluorography shows, at pushing the soil out in *Talpa* the anterior body part turns at right angles to the posterior one and its forelimbs move in the vertical plane shifting the earth to the surface from one side and planting firmly against substrate from another. The analogical description was made at the observations in nature (Hisaw, 1923; Reed, 1951). As a result the mobility in the thorax region has to be especially great. In this connection the reduction of the thoracic vertebrae high is noted (Platonov, 2002). The biomechanical analysis of burrowing in *Talpa* indicates if the pressure line of one hand during a “lateral thrust” misses the area of the pressure of the opposite hand, for the movement some other mechanisms of the support have to act (Nikol'skii, 1978). It may be thorax, back and hindlimbs. The most frequently this support, probably, falls on thorax where in *Talpa* the corium cutis becomes the thickest. The process of throwing the soil out with the head results in the analogical adaptive changes of the head skin in *Spalax* and *Myospalax* (Gambaryan, 1989).

Table 6. Skin layer thickness on the thorax and head: A — subcutaneous muscle; B — cutis; C — epidermis (transverse section, in mm).

Species	Thorax			Head		
	A	B	C	A	B	C
<i>Rattus norvegicus</i>	0.09	0.31	0.22	0.16	0.31	0.16
<i>Spalax microphthalmus</i>	0.69	0.49	0.32	1.03	0.91	0.56
<i>Talpa europaea</i>	0.34	0.72	0.44	0.34	0.09	0.06

In *Talpa* the head skin is much thinner (cutis is eight times thinner and epidermis is seven times thinner) than on the thorax. In *Rattus* the skin thickness on the head and thorax is approximately similar and in *Spalax* the head skin is twice as thick as on the thorax (Tab. 6). Moreover, the skull of *Talpa* is rather thin and can not stand up to pressure which is 20 times more than body weight. In *Spalax* and *Myospalax*, on the contrary, the skull is hard with the crests well developed (Figs. 4 and 5). Thus, the morphofunctional analysis presented above indicates rather distinctly that *Talpa* is unable to throw the soil out with the head.

Conclusions

1) The structural peculiarities of the axis skeleton and muscles in the neck region of different burrowers are connected with their manners of digging. In *Rattus* unspecialized for burrowing activity the neck is characterized by sufficient mobility on the whole extent, in all intervertebral joints. In *Talpa* at the pushing the soil apart with forelimbs the drawing of head backwards is observed. It results in arched neck position, atlas being displaced on the ventral parts of the occipital condyles. At the drawing the head forward during the searching of food the role of *m. colli longus* is most important. For its insertion in *Talpa*, in contrast to such of other burrowers and *Rattus*, the specific ventral plates at the bases of the pleurapophyses are developed not only on the sixth, but also on the fourth-fifth cervical vertebrae. Meanwhile, on the whole the character of the intervertebral joints of the neck indicates the vertical mobility extent is similar to that of *Rattus*, but lateral displacements are more restricted on the second-seventh vertebrae. In *Spalax* and *Myospalax* the process of the throwing the soil out with the head becomes possible under conditions of the significant consolidation of the cervical vertebrae. The latter is arrived by the sharp decreasing of the mobility in the intervertebral neck joints up to their partial accretion. However, in comparison to *Rattus* and *Talpa*, the more high mobility is observed in the occipital joint region. The spinous process of axis is significantly enlarged overhead and thickened as strengthened brief muscles of occipital joint take the origin there.

2) The mode of throwing the soil out with the forelimbs in *Talpa* is connected with the turn of the

anterior body part at about right angles to the posterior part. It becomes possible under conditions of the specific mobility in the thoracic region, which is provided by the nearly whole lack of the spinous processes on the first nine thoracic vertebrae. In *Spalax*, *Nannospalax*, and *Myospalax* the specific character of the thoracic part is conditioned by ensuring of two contradictory requirements connected with their digging manners. On the one hand, at the throwing the soil with the head the increasing of the solidity for the neck support is required and on the other hand, the increasing of the spine mobility for the maneuvers into the narrow tunnels. As a result the specific withers from the series of elongated spines on the second-sixth (seventh) thoracic vertebrae are developed. Moreover, the great pressure from the neck region results in the increasing of solidity of the first thorax segment: the first rib is widened powerfully and accreted with the manubrium sterni. Meanwhile, the increasing of the caudal inclination of the spinous processes and their narrowing on the tips (in spalacids), leading to the enlarged distance between the spines, make possible the increasing of the mobility in the thoracic region.

3) The adaptation to the throwing the soil with the head in *Spalax*, *Nannospalax*, and *Myospalax* results in strengthening of the muscles taking part in this process: extensors of occipital and elbow joints; the muscles lifting the body between the forelimbs. All these muscles function also in the landing phase during the jump locomotion in *Rattus*. However, their force requiring for the damping of shocks is incomparably less than such which is necessary for the throwing the soil with the head. Therefore, all the main groups of the muscles in *Rattus* are about four–six times weaker than such in *Spalax*, *Nannospalax*, and *Myospalax*. Meanwhile, the extensors of occipital joint in *Talpa* are about 20 times weaker than those in spalacids and *Myospalax*. On the way, the increasing of the relative weight of mm. pectoralis in *Talpa* is connected with the specific mode of its burrowing activity. The latter consists in pushing the soil apart by the forelimbs, but not in lifting the body between the hands as in spalacids and *Myospalax*.

4) In the process of burrowing in *Talpa* the support on the thorax often takes place. It results in thickening of the skin, which on the thorax is about 20 times thicker than such on the head. At the burrowing activity of *Spalax*, *Nannospalax*, and *Myospalax* throwing the soil out with the head the support on the thorax is absent. In this connection their skin on the head is about 5–6 times thicker than such on the thorax, whereas in *Rattus* its thickness on the head and thorax is approximately equal.

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