FORMATION OF THE CORACOID REGION OF THE ANURAN PECTORAL GIRDLE

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The anuran pectoral girdle consists of the scapular and coracoid regions. The latter is composed of the coracoid, procoracoid, epicoracoid, and clavicular elements. The coracoid and procoracoid enclose a large coracoid fenestra, which is a unique feature of these amphibians. Despite many authors having studied the development of the amphibian pectoral girdles, some mechanisms of its development remain unclear. This paper presents a morphological description of the development of the coracoid part of the pectoral girdle in four anuran species (*Bombina bombina*, *Bufo bufo*, *Rana temporaria*, and *Xenopus laevis*) and proposes a mechanism of its ontogenetic formation. The critical part of this process seems to be the position and size of the coraco-clavicularis nerve, vein and artery complex.

Keywords: Anura, coracoid fenestra, epicoracoid, lymphatic cavity, ontogenesis, pectoral girdle.

INTRODUCTION

At the end of the nineteenth and beginning of the twentieth centuries, there was controversy among comparative anatomists about the development of the anuran pectoral girdle given the problematic homology of the pectoral girdle elements among tetrapods. The sticking point was the questionable mode of the formation of the coracoid fenestra — a large opening between coracoid and procoracoid. Gegenbaur (1898) and his followers (Fürbringer, 1900; Braus, 1909; de Villiers, 1924; van Gelderen, 1924; Nauck, 1929) described the fenestra as having resulted from a reduction of the central part of the common anlage of the coracoid and procoracoid. However, Götte (1877) and Fuchs (1922, 1926, 1927) thought that the fenestra was a by-product of the growth patterns of coracoid and procoracoid, the distal ends of which eventually meet one another. The number of anlagen involved in the development of the lower part of the anuran pectoral girdle was discussed too. In more recent literature, the development of the cartilaginous elements of the pectoral girdle has been repeatedly described, though still in few genera. The development of the pectoral girdle was investigated histologically in *Bombina orientalis*, *Bufo gargarizans*, and *Kaloula borealis*

(Hsiao, 1933 – 34); *Rana tigrina* and *Bufo andersoni* (Bhati, 1961); *Rana temporaria* and *Bufo bufo* (Griffiths, 1963). Wiens (1989) investigated tadpoles of *Spea bombifrons* double-stained for bone and cartilage. Púgener and Maglia (1997) described the development of the pectoral girdle on double-stained whole-mounts of tadpoles of *Discoglossus sardus*, whereas Havelková and Roček (2006) examined the same species histologically. Shearman (2005, 2008) recently added to our knowledge of development in *Rana pipiens*, *Xenopus laevis*, and *Bombina orientalis*. However, it was only Kaplan (1993) who returned to discussion about the mechanisms of formation of the coracoid fenestra based on his description of the pectoral girdle development in *Rana blairi* and *Bufo woodhousii*.

Numbers of anlangen concerned early researchers, but tissue types (i.e., cartilaginous or mesenchymal) were never clearly defined. For instance, Braus (1909) and Nauck (1929) described separate centers of chondrification for the coracoid and the procoracoid, and they mentioned a common mesenchymal anlage of the scapulocoracoid. Thus, we can infer that they considered the formation of the coracoid fenestra to occur "within" the common coracoid plate. In contrast, Götte (1877) and Fuchs (1922, 1926, 1927) discussed the formation of the coracoid fenestra to occur "outside" of the coracoid plate, though at a later stage, when the discontinuity of the coracoid and the procoracoid was already evident.

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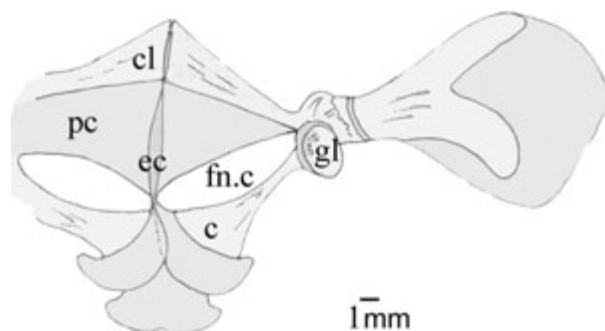
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Fig. 1. Structure of anuran pectoral girdle in the pipid frog, *Xenopus laevis*. **Abbreviations:** c, coracoid; cl, clavicle; ec, epicoracoid; fn.c, coracoid fenestra; gl, glenoid cavity; pc, procoracoid.

Regarding the number of anlagen for a structure one needs to define what type of tissue we discuss. All anlagen of the amphibian pectoral girdle arise from cells of the lateral plate mesoderm; therefore, all the elements of the girdle arise from a single mesenchymal anlage. However, the number of chondrification centers is not the same in caudates and anurans. In salamanders, the entire pectoral girdle develops from a single cartilaginous anlage (Borkhvardt and Baleeva, 2002), whereas in some anurans, just the scapular part of the pectoral girdle has two chondrification centers (Baleeva, 2001; Shearman, 2005). Herein, I present evidence for the number of cartilaginous anlagen in the lower or ventromedial part of the anuran pectoral girdle. As soon as this question has arisen in the context of a discussion of the mechanism of formation of the coracoid fenestra — a unique characteristic of anurans — this process also is addressed.

MATERIAL AND METHODS

The formation of the cartilaginous elements of the coracoid part of the pectoral girdle was examined in four species of Anura: the fire-bellied toad, *Bombina bombina* (Bombinatoridae) — 22 larvae; *Xenopus laevis* (Pipidae) — 27 larvae; *Rana temporaria* (Ranidae) — 52 larvae; and *Bufo bufo* (Bufonidae) — 46 larvae. Larvae from the age of early forelimb buds through metamorphosis were used.

The egg clutches of the *Rana temporaria* and *Bufo bufo* were collected in vicinity of St. Petersburg. The eggs of *Bombina bombina* were obtained with artificial hormonal stimulation in the laboratory from animals caught in the Belgorod oblast' of Russia (for details, see Borkhvardt and Malashichev, 2001). *Xenopus laevis* also was hormonally stimulated for breeding as de-

scribed by Detlaf and Rudneva (1975). All larvae were reared in the laboratory by standard techniques (Dabagian and Sleptsova, 1975; Ivanova and Piastolova, 1979; Lang, 1988/89). The larvae of *X. laevis* were staged according to normal tables by Nieuwkoop and Faber (1956); larvae of other species were staged according to normal tables for *Rana temporaria* by Dabagian and Sleptsova (1975). For histological examination, the tadpoles of all ages were sacrificed in Bouin's fixative, transferred through an alcohol series of the increasing concentrations, and embedded in paraffin. Serial sections of 7 – 13 µm thickness were made in three planes — transverse, frontal, and parasaggital — and stained with hematoxylin according to Delafild or Harris and eosin. For better cartilage visualization, additional staining with Alcian Blue was used on the same sections.

The nomenclature of muscle, nerves, and blood vessels follows that of Gaupp (1896, 1899), and Nozdrachev and Poliakov (1994). We used the taxonomy of order Anura according to Frost et al. (2007). Microphotographs are made with the digital microscopic video-imaging system "VideoTesT®-2200."

RESULTS AND DISCUSSION

**Formation of the Lower "Frame"
of the Pectoral Girdle**

The coracoid fenestra (*foramen obturatorum* [Braus, 1909] *seu fenestra scaphoides* [Fuchs, 1926]) is bounded with three skeletal elements: coracoid, procoracoid, and epicoracoid (Fig. 1), which together form a frame-like construction. Hereinafter we call this construction the "frame."

Gegenbaur (1898) and his followers (Fürbringer, 1900; Braus, 1909; de Villiers, 1924; van Gelderen, 1924; Nauck, 1929) thought that the ventral elements of the pectoral girdle in all vertebrates formed by the reduction of the central part of the common coracoid plate and the subsequent transformation of the cell material into the obturator membrane of the coracoid fenestra. Fürbringer (1874) described a nerve, the *nervus supracoracoideus* that passes through the coracoid fenestra of anurans; Gaupp (1896) renames the nerve as the *nervus coraco-clavicularis*. Braus (1909) and Nauck (1929) described the formation of the coracoid fenestra as a process of dilating the opening for the nerve in the coracoid plate. Ventral elements of the pectoral girdle (i.e., the coracoid, procoracoid, and epicoracoid) chondrofy from the mesenchymal anlage surrounding the coracoid fenestra. Kaplan (1993) suggested that several modes of

formation of three separate elements from a single sca-
pulocoracoid anlage could exist. On the one hand, dur-
ing the formation of the coracoid fenestra (as he writes,
may be by means of cell death) a mechanical separation
of the scapulocoracoid on coracoid, procoracoid, and
epicoracoid takes place. On the other hand, along with
this process, the mesenchymal cells on the periphery of
the scapulocoracoid differentiate and form the three car-
tilaginous elements.

Götte (1877) and Fuchs (1922, 1926, 1927), who in-
vestigated the development of the larvae of *Rana tempo-
raria*, concluded that the procoracoid is a ventral pro-
cess of the scapula, whereas the coracoid arises from its
own anlage. A characteristic spatial position of the carti-
laginous anlagen in the ventral part of the pectoral girdle
on a certain developmental stage ("die Zange" — in the
form of pincers) determines the existence of a gap
between them, which after the contact of the distal ends
of procoracoid and coracoid becomes closed into a cora-
coid fenestra.

Before Stage 42 in *Rana temporaria*, *Bufo bufo*, and
Bombina bombina there is no recognizable anlages of
pectoral girdle elements. Basing on data of light-micros-
copy sections we can mark out only a huge group of me-
senchyme cells which later will give rise to lower part of
pectoral girdle and muscles connected with it. It is situ-
ated at the base of forelimb bud under humerus anlage
(Fig. 2). However, even before the mesenchymal con-
densations of the coracoid and procoracoid are visible
(as early as Stage 41), the region of the presumptive
coracoid fenestra can be seen in sections in all the three
species; it is marked by coraco-clavicularis nerve, artery,
and vein (Figs. 2, 3*a*, *b*). Each is directed almost strictly
dorsoventrally, turns around the proximal end of the
humerus, and then, at the level of the ventral quarter of
the base of the limb bud, bends smoothly laterally. At
Stages 42 and 43, mesenchymal condensations form cra-
nially and caudally to this neurovascular complex. The
procoracoid forms anteriorly as an elongated, rodlike
dorsoventrally oriented mesenchymal condensation; the
condensation of the coracoid is similar shape and orien-
tation, but located posteriorly. Even at this stage, the
coracoid is more massive than the procoracoid. The di-
ameter of the nerve is so large, that it is comparable to
sizes of the mesenchymal condensations of the coracoid
and procoracoid (Fig. 3*a*, *c*).

By Stage 44, matrix accumulation begins in the up-
per parts of the coracoid; it occurs slightly later in the
procoracoid condensation. The mesenchymal depres-
sion becomes noticeable around the blood vessels of the
coracoid region (Fig. 4*a*, *b*). This local depression is
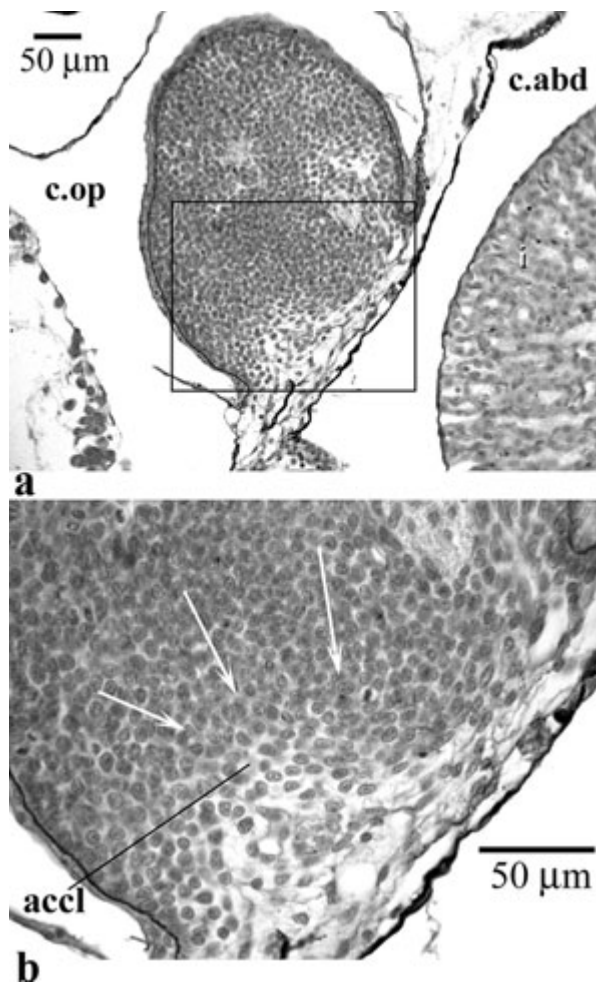slender, and the mesenchyme at the level of the ventral

Fig. 2. Fragment of a frontal section of the right coracoidal part of
pectoral girdle in *Rana temporaria* larvae at Stage 41 (*a*); (*b*) the
same, enlarged. The head is on the left. The arrows show mesenchyme
of the coracoidal part of pectoral girdle. **Abbreviations:** accl, arteria
coraco-clavicularis; c.abd, abdominal cavity; c.op, opercle; i, gut.

parts of the coracoid and procoracoid condensations is
not involved (Fig. 4*a*, *b*). By Stage 45, the coracoid and
procoracoid elongate and lie almost parallel to one an-
other; their upper parts are chondrified. A loose mesen-
chyme through which nerves and blood vessels pass lies
between the two anlagen. The diameters of the coracoid
and procoracoid now are much larger than that of the
coraco-clavicularis nerve; the nerve, together with the
artery and vein of the same name, lie almost perpendicu-
lar to the upper levels of these cartilaginous under the
glenoid cavity (Fig. 4*c*, *d*). Hence, the middle parts of
the coracoid and the procoracoid are separated from one
another only by a region of loose mesenchyme, under
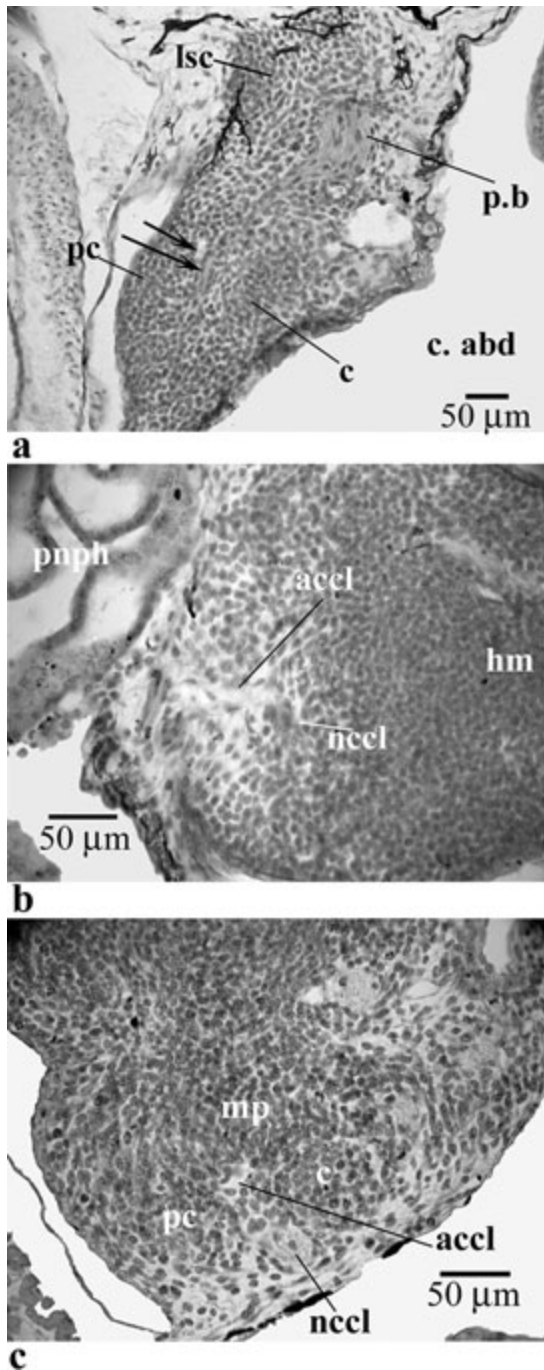which they turn into a dense mesenchymal mass. By

Fig. 3. Fragment of parasaggital section at the level of the base of the limb bud in *Bufo bufo* larvae at Stage 42 (*a*). The arrows show the nervus coraco-clavicularis (dark) and the arteria coraco-clavicularis (light). Fragment of a transverse section at the level of the base of the limb bud in *Rana temporaria* larvae at Stage 41 (*b*). Fragment of a frontal section in the right coracoidal part of the pectoral girdle region in *Rana temporaria* larvae at Stage 43 (*c*). The head is on the left. **Abbreviations:** hm, humerus; lsc, lower-scapular condensation; mp, musculus pectoralis; nccl, nervus coraco-clavicularis; p.b, plexus brachialis; pnph, pronephros. See Figs. 1 and 2 for other abbreviations.

Stages 46 and 47, the coracoid, and slightly later the procoracoid become covered with perichondrium. The cartilage is hypertrophied in the middle of coracoid, with the diameter of the coracoid being greater (~1.5 – 2×) than that of the procoracoid (Fig. 5). The coracoid fenestra with a lymphatic cavity appears between the anlagen; it extends from the glenoid cavity and ventrally to the middle of the coracoid; the lower part of the fenestra is filled with loose mesenchyme (Figs. 5 and 6). At Stages 47 and 48, the mesenchyme, which continues the cartilaginous anlagen, is starting to chondrify from above, and forms an arc, which joins the coracoid and the procoracoid. By the onset of the metamorphosis (Stage 49), the coracoid of each species examined acquires endochondral bone, starting from its middle part. At the height of metamorphic climax (Stages 51 and 52) the contralateral halves of the girdle meet midventrally. By Stage 52, the lymphatic cavity occupies the whole coracoid fenestra.

In *Xenopus laevis*, the mesenchymal anlagen of the skeletal elements of the pectoral girdle become visible at Stage 53/54, which correspond approximately to Stage 44/45 for *Rana temporaria*. At this time, only the lower scapular and coracoid accumulations occur. The procoracoid accumulation is not yet formed and this region is occupied by loose pack of mesenchyme. It is possible to determine only caudal border of future procoracoid which is marked by coraco-clavicularis artery and large nerve runnig craniad to the coracoid accumulation and under the prospective glenoid cavity. However, the procoracoid overtake the coracoid in the degree of tissue maturation; at Stage 55, the lymphatic cavity is being formed (in the presumptive upper part of the coracoid fenestra) around the coraco-clavicularis artery and the procoracoid starts to chondrify (Fig. 7), although its diameter is still less than that of the coracoid. The procoracoid adds mesenchyme mostly along its anterior edge, thereby assuming the shape of a rather narrow plate. Thus, characterization of the common anlage of the pectoral girdle in *Bombina bombina* and *X. laevis* as scapulocoracoid (Hsiao, 1933 – 1934; Kaplan, 1993) is a warrantable assumption. Because the humerus in *B. bombina* approaches the cranial part of the coracoid and the region of the prospective coracoid fenestra (i.e., behind the procoracoid), the procoracoid appears to be continuation of the so-called, lower scapular anlagen (Baleeva, 2001), which is situated anterodorsal to the proximal end of the humerus. In *X. laevis*, the humerus approaches the anlagen of the pectoral girdle cranially from the coracoid; therefore, at the mesenchymal anlagen stage, the coracoid resembles a continuation of the lower scapular accumulation. However, both in *B. bom-*
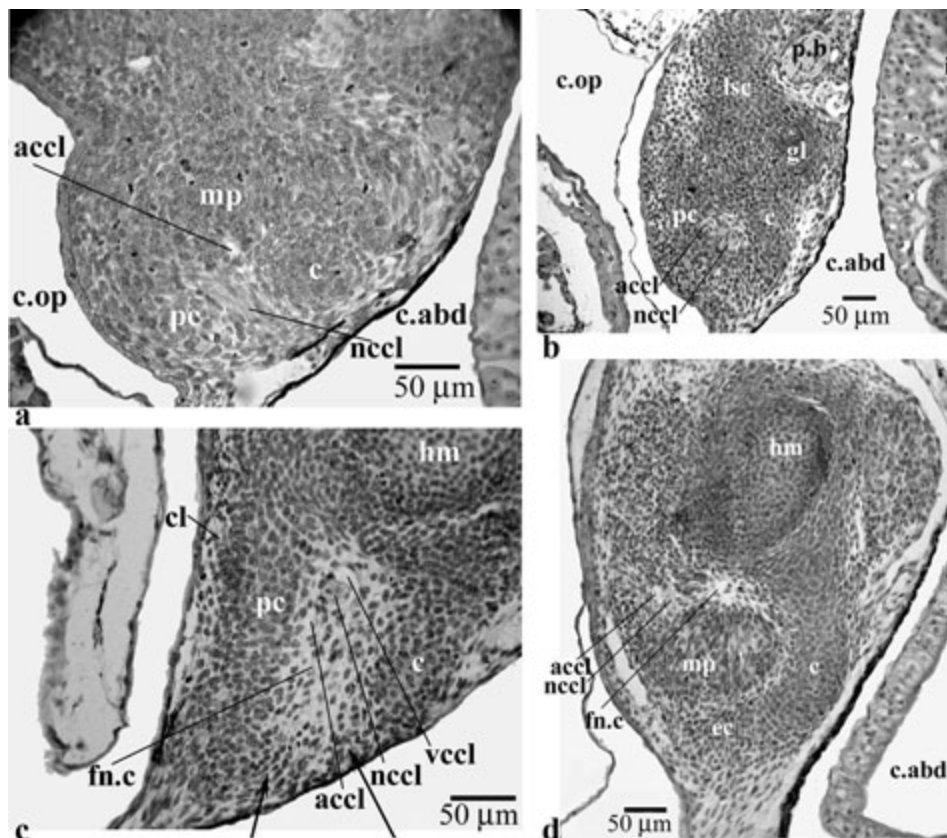
Fig. 4. Fragment of parasaggital (*a*) and frontal (*b*) sections of the right coracoidal part of the pectoral girdle region in *Rana temporaria* larvae at Stage 44; fragment of parasaggital section of the coracoidal part of pectoral girdle region in *Bufo bufo* larvae at Stage 45 (*c*). The arrows show general mesenchyme of the coracoid and procoracoid. Fragment of a parasaggital section of the coracoidal part of pectoral girdle region in *Rana temporaria* larvae at Stage 45 (*d*). The head is on the left. **Abbreviations:** fn.c, coracoid fenestra; vccl, vena coraco-clavicularis. See Figs. 1 – 3 for other abbreviations.

bina and *X. laevis*, the cartilage arises from three centers around the proximal humerus; therefore, we should consider at least three anlagen of the pectoral girdle in these species. The neurovascular complex passes deeply ventral to the glenoid cavity; therefore, the mesenchyme deep to the glenoid cavity is common for both the coracoid and the procoracoid anlagen. The mesenchyme that lies under the lymphatic cavity of the coracoid fenestra also is common for them. The middle parts of both skeletal elements are covered by perichondrium from Stage 56.

In *Xenopus laevis*, as well as in other anurans studied, the gigantic coraco-clavicularis nerve (at early stages) and the corresponding artery and vein (at later stages) determine the formation of two separate anlagen of the ventral part of the pectoral girdle. They probably represent a mechanical obstacle, which prevents the formation of a single mesenchymal anlage in this region of the embryo. Borkhvardt (1992, 1994) noticed that the to-
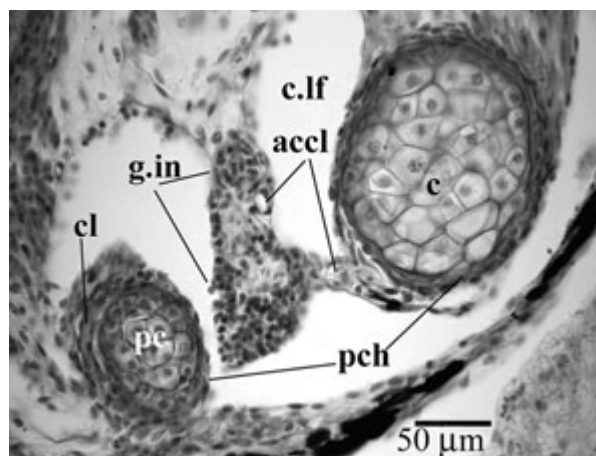

Fig. 5. Fragment of a frontal section of the right coracoidal part of the pectoral girdle region in *Rana temporaria* larvae at Stage 48. The head is to the left. **Abbreviations:** c.lf, lymphatic cavity; g.in, coracoidal glande; pch, perichondrium. See Figs. 1 – 4 for other abbreviations.
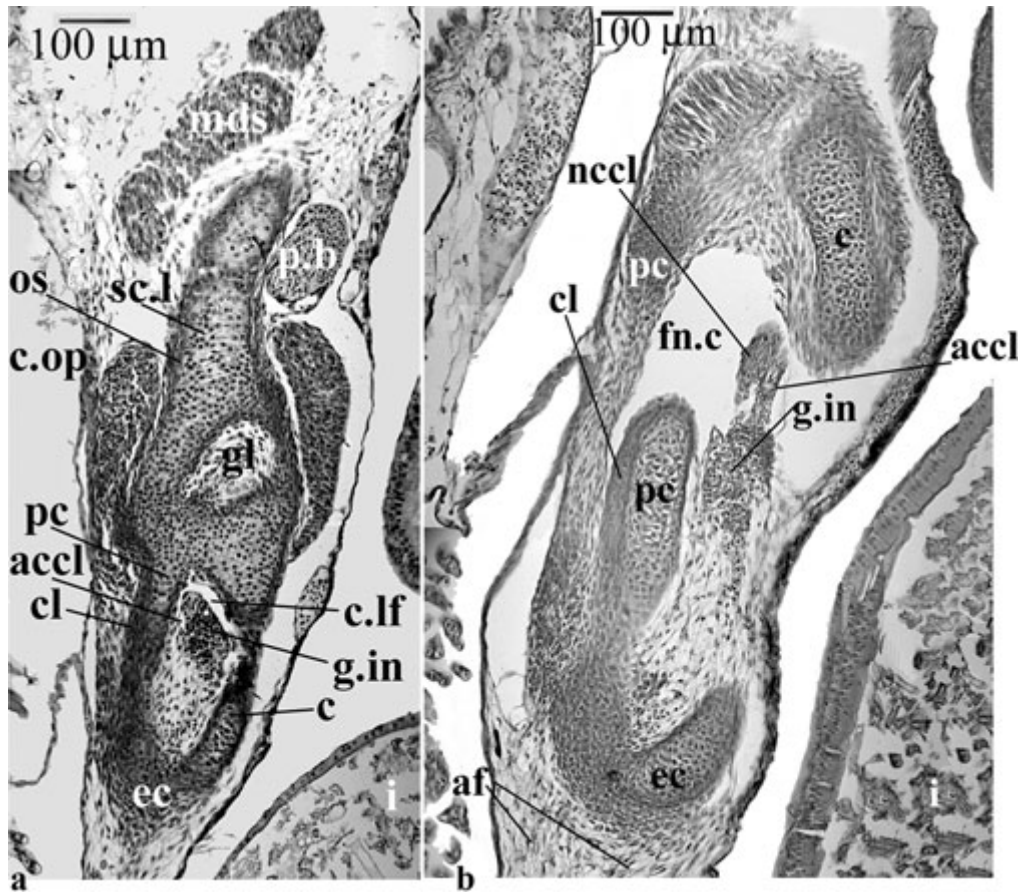
Fig. 6. Fragments of parasaggital sections of the coracoidal part of the pectoral girdle region in *Rana temporaria* larvae at Stages 47 (*a*) and 48 (*b*). The head is on the left. See Figs. 1 – 5 for abbreviations.
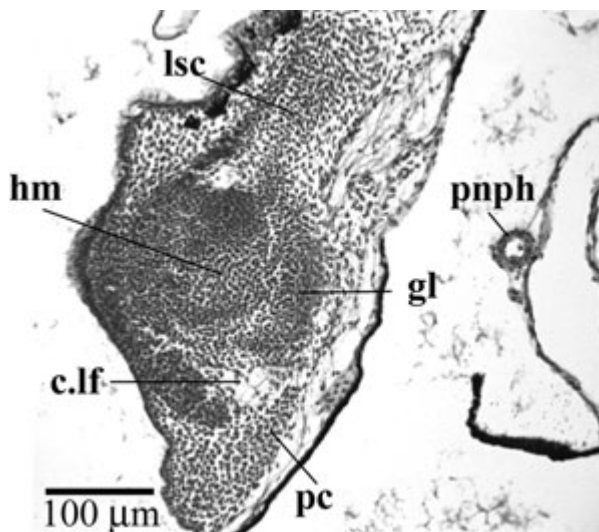

Fig. 7. Fragment of a transverse section of the right coracoidal part of the pectoral girdle region in *Xenopus laevis* larvae at Stage 55. See Figs. 1 – 5 for abbreviations.

pography of the blood vessels in the limb bud of the salamanders correlates to the borders of the prospective skeletal elements of the zygopodium. He suggested, that the blood vessels "separate groups of skeletogenous cells." In the case anurans, we observe a similar phenomenon during formation of the coracoid fenestra, when mesenchymal condensations appear on each side of the coraco-clavicularis artery and vein.

Later, the coracoid fenestra forms between the anlagen of the coracoid and the procoracoid. Braus (1909) first noticed the neurovascular "*foramen*" (Gefäßnervenloch) in the region where the coracoid fenestra forms. However, he thought that the coracoid nerve played the leading role in the formation of the fenestra and he paid no attention to the adjacent blood vessels.

My data show that there is a depression of mesenchyme near the coraco-clavicularis artery and vein; this depression later develops into a lymphatic cavity. Wilting et al. (1999) and Schneider et al. (1999) showed that

lymphatic vessels and cavities in chick embryos develop in coordination with embryonic blood vessels. In the case of lymphatic cavity formation between the anlagen of the coracoid and the procoracoid, it is logical to propose that formation is correlated with the presence of the claviculo-coracoid vein. The size of this cavity prevents the fusion of the coracoid and procoracoid anlagen. The evidence of its role as an obstacle could be the fact, that the ends of the coracoid and procoracoid anlagen are united in the common mesenchyme ventrally beyond the limits of the lymphatic cavity; chondrification of this mesenchyme forms a bridge between the coracoid and the procoracoid — the so-called epicoracoid. Because this bridge forms the ventral margin of the coracoid fenestra, its formation is described in detail below.

Epicoracoid Formation

Parker (1868) first used the term "epicoracoid" ("*epicoracoideum*") to describe the medial edge of the coracoid cartilage, and indistinctly indicated the border between the coracoid and the epicoracoid. Braus (1919) tried to define the epicoracoid as a part of the primary (or embryonic) cartilaginous pectoral girdle; thus, the coracoid ossifies, but the so-called cartilaginous part, which lies on the midline of the belly and remains unossified, is the epicoracoid. Moreover, Braus (1909) noted in experimental and developmental studies the pectoral girdle of *Bombina variegata* that this species lacks a separate center of chondrification in the epicoracoid.

Under the term "epicoracoid" I mean contacting each other medial borders of the contralateral halves of the pectoral girdle.

In the larvae of *Bufo bufo*, *Rana temporaria*, and *Bombina bombina*, the region of the prospective epicoracoid is evident at Stage 44. One part of the pectoral muscle (*m. pectoralis pars epicoracoidea*) inserts along the free edge of the epicoracoid; therefore, the region where the epicoracoid first appears can be marked by the appearance of this early-developing muscle even in young larvae (Fig. 4*d*). It remains the marker of the epicoracoid in later development.

In Stages 45 and 46 *Bufo bufo*, the mesenchyme that continues the coracoid cartilage goes along the front wall of the visceral cavity and forms an angle of about 130° with the tip of the coracoid owing to the configuration of the space under the base of the forelimb bud. The mesenchyme continues the procoracoid cartilage along its longitudinal axis (Figs. 4*c*, 8*a*). Underneath the forming coracoid fenestra, the edge mesenchyme of the procoracoid and the coracoid merge in the common mass (Fig. 8*a*). The *m. pectoralis* attaches to the medial side

of the coracoid and to the common mesenchyme of the coracoid and the procoracoid. The length of the cartilaginous part of the procoracoid is greater than the length of the cartilaginous part of the coracoid. These cartilages are positioned nearly parallel to one another and pass from the glenoid cavity anterolaterally. At the next stage, the common mesenchymal mass of the coracoid and the procoracoid chondrifies ventrally to the distal parts of these elements; more ventrally, it becomes looser and ends with a thin layer of cells in the gap between the outer wall of the body and the wall of the visceral cavity. By Stage 48, the coracoid and the procoracoid are bridged by the cartilaginous epicoracoid.

In *Bombina bombina*, the base of the forelimb bud is oriented in such a way that the coracoid and the procoracoid are directed from the glenoid cavity at different angles — the coracoid more abrupt anterolaterally such that in its lower part it appears laterally to the procoracoid. The space between the frontal body wall and the visceral cavity narrows downward, the coracoid and procoracoid become thin and the mesenchyme of their tips merges (Fig. 8*b*). This mesenchymal arc, which joins the coracoid and the procoracoid, is oriented almost perpendicular to the longitudinal axis of the body. The anlage of the *m. pectoralis p. epicoracoidea* comes close to it. The coracoid and the procoracoid begin to chondrify at nearly the same time; however, the difference in the chondrocyte size between these elements soon becomes evident, chondrocytes of the coracoid being larger (Fig. 8*c*). By Stage 49, the common mesenchyme of the two elements chondrifies to form the epicoracoid.

In *Rana temporaria*, the coracoid anlage is situated more lateral than that of the procoracoid. However, because the base of the forelimb bud is angled to the longitudinal body axis, coracoid and procoracoid actually lie approximately parallel to the longitudinal body axis. The coracoid anlage stretches along the wall of the visceral cavity and is oriented anteroventrally. The procoracoid anlage extends downward anteriorly along the cranial wall of the base of the limb bud. The coracoid chondrifies at Stage 44 in the region of glenoid cavity, whereas the procoracoid forms cartilaginous matrix only in its upper part (Fig. 4*a*, *b*). The anlage of the pectoral muscle is adjacent to the mesenchyme, which continues the coracoid anlage. At Stage 45, the cartilaginous coracoid anteriorly convex in shape and is joined to the procoracoid cartilage by mesenchyme, which we term "the epicoracoid" (Fig. 4*d*). The mesenchyme that continues the coracoid craniad (i.e., the mesenchyme of the posterior part of the epicoracoid) starts to chondrify. At Stage 47, the anterior part of the coracoid — the epicora-
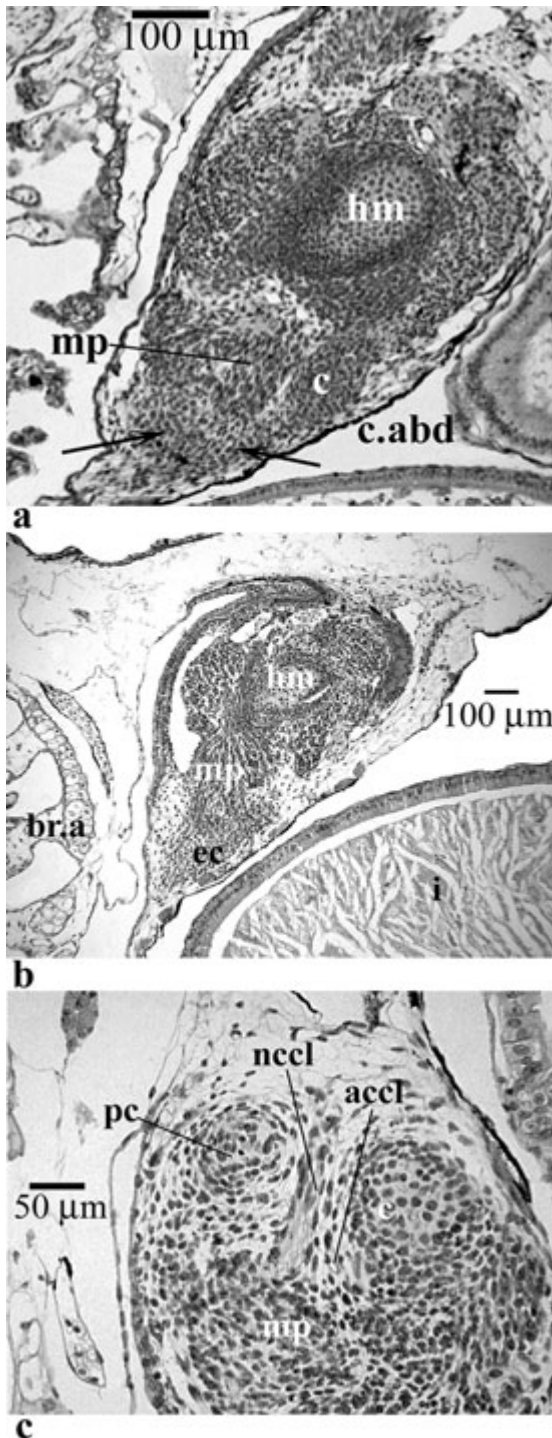
Fig. 8. Fragment of parasaggital section of the coracoidal part of the pectoral girdle region in *Bufo bufo* larvae at Stage 46 (*a*). The arrows show general mesenchyme of coracoid and procoracoid. Fragment of parasaggital (*b*) and frontal (*c*) sections of the left coracoidal part of the pectoral girdle region in *Bombina bombina* larvae at Stage 46. The head is on the left. **Abbreviations:** br.a, gill arch. See Figs. 1 – 5 for other abbreviations.

coid — is almost completely cartilaginous; however, the cartilaginous arc is not continuous to the procoracoid because the most anterior part of the epicoracoid is composed of the mesenchyme (Fig. 6*a*). By Stage 48, the epicoracoid is completely chondrified and arcuate, joining the coracoid with the procoracoid (Fig. 6*b*). But Götte (1877) and Fuchs (1927), who studied the development of *Rana temporaria*, concluded that the epicoracoid cartilage is formed by the flattened distal ends of the coracoid and the procoracoid.

Griffiths (1963) assumed that the epicoracoid forms from part of the coracoid that rapidly grows anteriorly. Tyson (1987 as cited by Kaplan, 1993) agreed with the Griffiths' conclusions based on her investigations of the development of *Pseudacris triseriata*, *Spea bombifrons*, *Bufo boreas*, and *Rana sylvatica*. Kaplan (1993) described the formation of the epicoracoid in *Rana blairi* and *Bufo woodhousii* as chondrification of cells in the lower part of the coracoid and the procoracoid. However, as chondrification begins earlier in the coracoid, then it is the very element, which forms epicoracoid. He also noticed that at a certain developmental stage, there are no borders between the three elements; they form later, following the shape of the coracoid ossification. Havelková and Roček (2006) concluded the epicoracoid of *Discoglossus sardus* is produced by the procoracoid.

It is possible to formulate that the anuran epicoracoid is the cartilaginous arc that joins the distal ends of the coracoid and the procoracoid. The course of its development might differ among species owing to the differences in distribution of the mesenchyme, which lies ventral to the coracoid and the procoracoid anlagen, as well as to difference in the onset of chondrification of these elements. The greater contribution to the epicoracoid of one or the other depends on the onset of chondrification begins in both elements; in *Bufo bufo* and *Bombina bombina*, the onset of chondrification in both the coracoid and the procoracoid occurs almost simultaneously and both elements contribute equally to the epicoracoid. In *R. temporaria* (own data), the process of chondrification of the coracoid starts much earlier; hence, the epicoracoid is formed mostly by the elongated cartilaginous distal edge of the coracoid.

CONCLUSIONS

The ventral, coracoid, part of the pectoral girdle of anurans has two cartilaginous anlagen, which arise on each side of *nervus*, *vena et arteria coraco-claviculares*. Probably, the position of the neurovascular complex determines heterogeneity of the mesenchyme in this region, and by this, creates the necessary prerequisites for

development of two separate elements (see Borkhvardt, 1994). At early stages, the diameter of the nerve is proportional to the diameter of these mesenchymal accumulations, and, probably, the nerve serves the role of a physical factor, which prevents their fusion. At later stages, the coracoid fenestra acts as an obstacle between the skeletal anlagen to maintain a large lymphatic cavity around the artery and vein. During metamorphosis, when the procoracoid and coracoid enlarge, the coracoid fenestra is not healing, because of the formation of perichondrium, and later, of endochondral bone at the mid-length of the coracoid. In this regard, following of Gegenbaur were right in their observation that the primary character of the coracoid fenestra in relation to the formation of the lower "frame" of the pectoral girdle. Hence, the formation of the coracoid fenestra determines the topography of the elements in the coracoid part of the pectoral girdle in Anura.

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