Comparative osteology of *Acanthodraco dewitti* and relationships within the gymnodraconins (Pisces: Bathydraconidae)

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The structure of the bony skeleton of the recently described monotypic genus *Acanthodraco* Skora was examined and compared with that of two other monotypic genera of the subfamily Gymnodraconinae, *Psilodraco* and *Gymnodraco*. It is found that the genus *Acanthodraco* is clearly distinguished from two other genera by the separated lateral ethmoids, hook-like shape of the sphenotic, lack of the articulation between the prootic and intercalar, absence of the hook-like process of the hyomandibular and presence of additional spines on the opercular bones. In the osteological characters *Acanthodraco* is more related to *Psilodraco* than to *Gymnodraco*. Evolutionary trends in the gymnodraconins are discussed.

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Until recently, two monotypic genera, *Psilodraco* and *Gymnodraco*, were known in the subfamily Gymnodraconinae (Andriashev, 1983; Andriashev & al., 1989; Balushkin & Voskoboinikova, 1995). Recently a new genus and species *Acanthodraco dewitti* has been described (Skora, 1995). We examined the osteology of *A. dewitti* and compared it with that of *P. breviceps* Norman and *G. acuticeps* Boul. The phylogenetic relationships of these three genera are discussed.

Material and methods

The osteology of *A. dewitti* was studied on 2 specimens, SL 129.2 and 136.5 mm, from the collection of the Hel Marine Station of the Gdansk University (Poland). The osteological preparations were made following the method by Potthoff (1984). The structure of the axial and caudal skeleton has been examined on radiographs of 14 specimens of *A. dewitti*. We also used osteological preparations of 5 specimens of *G. acuticeps*, SL 174.9-348.5 mm, and 3 specimens of *P. breviceps*, SL 135.0-189.0 mm, from collection of the Zoological Institute of Russian Academy of Sciences.

Results

Neurocranium (Fig. 1). The shape of the neurocranium of *A. dewitti* is rather similar to that of *P. breviceps* (Voskoboinikova, 1988a, Fig. 1) in the relatively narrow ethmoidal region and interorbital space (Table 1), shortened posterior lateral ethmoid and sphenotic, ventrally curved vomer, sharply curved anterior limb of the parasphenoid and high mesethmoid as compared with that of *G. acuticeps* (Voskoboinikova, 1988a, Fig. 2). Previously it has been shown that all noted characters are plesiomorphies of the bathydraconids (Voskoboinikova, 1988a, 1988b; Andriashev & 1989).

However, there are some important differences between *A. dewitti* and *P. breviceps* concerning the position and shape of some bones. In particular, *A. dewitti* is characterized by the narrower vault of the skull and interorbital space, and longer ethmoidal region with longer vomer (Table 1). In *A. dewitti*, the anterior and posterior lateral

Table 1. Osteological characters of the gymnodraconins

Characters	*Gymnodraco*	*Psilodraco*	*Acanthodraco*
Ratio bone length/neurocranium length, %			
mesethmoid	40.5–44.0 / 41.8	31.1–35.8 / 34.0	30.0–33.0 / 31.5
vomer	31.4–37.0 / 34.3	20.0–24.7 / 22.9	27.8–30.0 / 28.9
premaxilla	49.0–53.2 / 51.7	44.5–46.2 / 45.6	44.4–50.3 / 47.3
lower jaw	77.6–79.8 / 79.0	73.2–75.6 / 74.4	70.0–72.2 / 71.1
hyoid arch	61.4–68.2 / 66.4	69.2–75.6 / 72.9	70.0–70.3 / 70.1
cleithrum	62.3–73.1 / 68.4	81.5–88.5 / 84.9	70.3–80.0 / 75.1
Ratio width/length of neurocranium at the level of			
sphenotic	46.0–50.8 / 48.4	62.1–68.4 / 65.1	46.7–63.3 / 55.0
interorbital space	19.8–21.4 / 20.7	15.2–16.8 / 16.2	14.4–16.6 / 15.5

ethmoids are separated by the cartilaginous bar, as in *G. acuticeps*, in difference to *P. breviceps* in which these bones are contiguous. It was shown that the separation of the ethmoids is among principal directions of the evolution of the bathydraconids and is associated with the lengthening of the ethmoidal region (Iwami, 1985; Voskoboinikova, 1988b; Andriashev & al., 1989; Balushkin & Voskoboinikova, 1995). So, we consider the separated ethmoids in *A. dewitti* and *G. acuticeps* as a synapomorphy. An autapomorphy of *A. dewitti* is the presence of hook-like lateral ridge of the sphenotic, in contrast to two other genera in which the sphenotic ridge is trapezoid. In *P. breviceps* and *G. acuticeps*, the intercalar is rather well developed and articulates with prooticum anteriorly (Voskoboinikova, 1988a, Fig. 1, 2). In *A. dewitti*, the intercaler does not articulate with the prooticum and is separated from this bone by the pterotic and exoccipital. This character is also advanced for the bathydraconids and occurs in *Parachaenichthys* and *Cygnodraco* of the bathydraconins only (Voskoboinikova, 1988b).

Infraorbitals (Fig. 2a). *A. dewitti* has two infraorbitals, the lacrimal and infraorbital 4, separated by a large interruption. Similar structure of the infraorbitals is found in *P. breviceps* (Voskoboinikova, 1988a) and in few other nothotenioids, and is considered most advanced among the notothenioids (Andriashev & Jakubowski, 1971; Jakubowski, 1971). *G. acuticeps* has a more primitive structure of the infraorbitals: four infraorbitals with small interruption between infraorbitals 2 and 3.

Splanchnocranium (Fig. 2b-e). In the structure of the splanchnocranium, *A. dewitti* is also more similar to *P. breviceps* both in the ratios and in the structure of various bony elements (Tabl. 1). Both species are similar in the moderate length of the jaws, vertical position of the ascending process of the premaxilla, presence of 1-2 enlarged teeth at the symphysis of the premaxilla and enlarged teeth in the posterior half of the dentary. In contrast to *G. acuticeps*, these two species are characterized by the rather broad palate with well-developed capitulum, covering two-thirds of the ectopterygoid, moderate size of the hyomandibular and narrow interstitial part of the preopercle. These characters, except for the teeth structure, can be

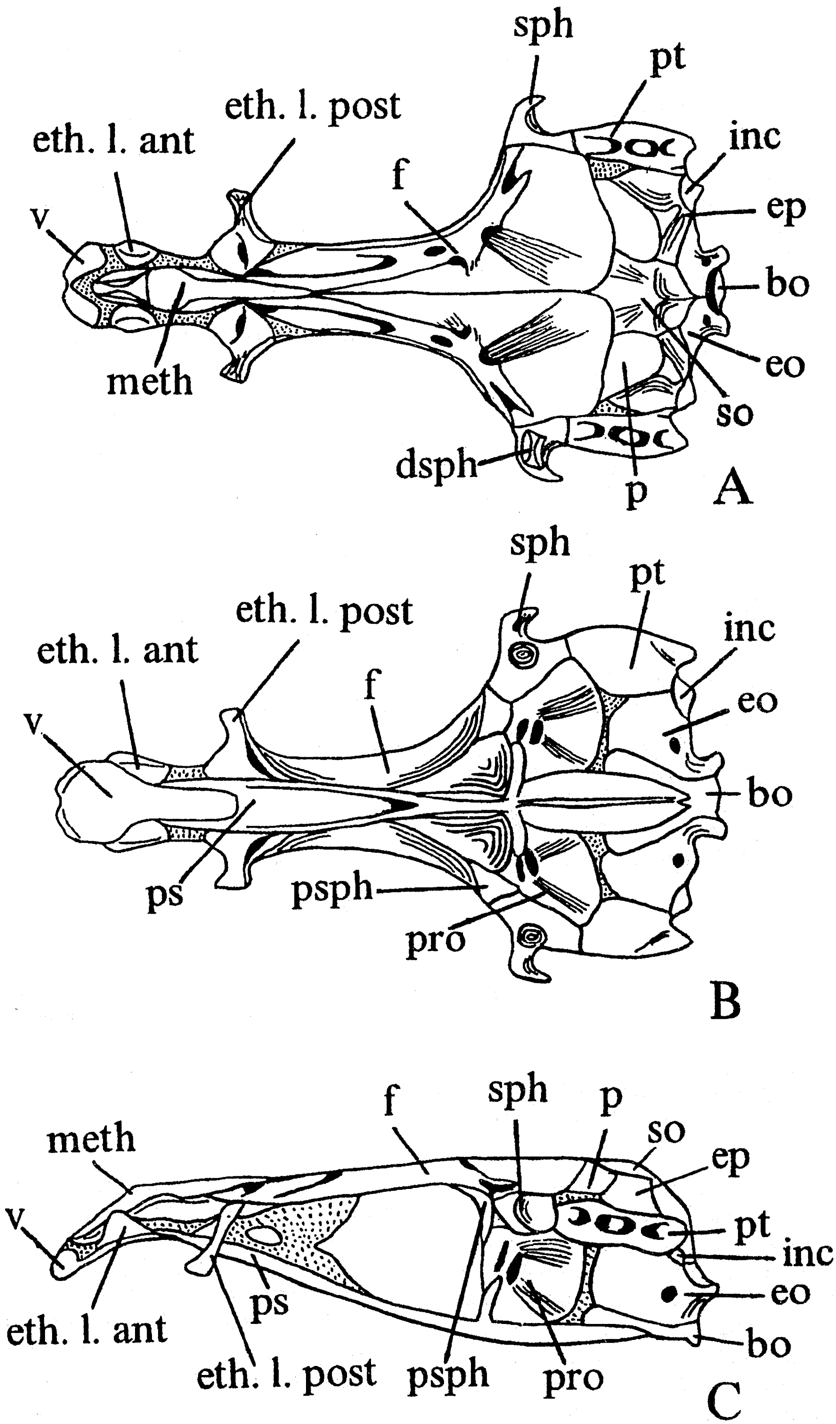

Fig. 1. Neurocranium of *Acanthodraco dewitti*, dorsal (A), ventral (B) and left lateral (C) views. *bo*, basioccipital; *dsph*, dermosphenoticum; *eo*, exoccipital; *eo*, epiotic; *eth. l. ant*, anterior lateral ethmoid; *eth. l. post*, posterior lateral ethmoid; *f*, frontal; *meth*, mesethmoid; *p*, parietal; *ps*, parasphenoid; *pt*, pterotic; *psph*, pterosphenoid; *so*, supraoccipital; *sph*, sphenotic; *v*, vomer. Cartilage stippled, ossifying white.

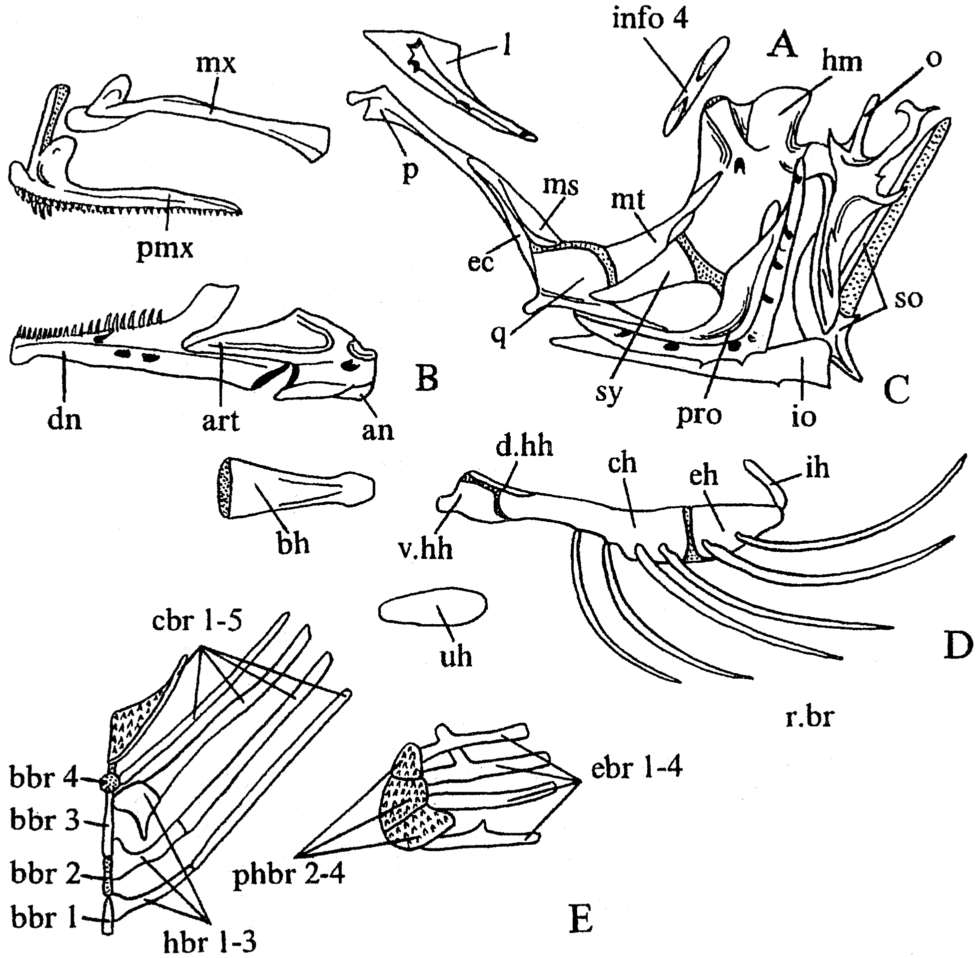

Fig. 2. Infraorbitals (A) and splanchnocranium (B-E) of *Acanthodraco dewitti*. *an*, angular; *art*, articular; *bbr 1-4*, basibranchials 1-4; *bh*, basihyal; *cbr 1-5*, ceratobranchials 1- 5; *ch*, ceratohyal; *d. hh*, dorsal hypohyal; *dn*, dentary; *ebr 1-4*, epibranchials 1-4; *ec*, ectopterygoid; *eh*, epihyal; *hbr*, hypobranchials 1-3; *hm*, hyomandibular; *ih*, interhyal; *info 4*, infroorbital 4; *io*, interopercle; *ms*, mesopterygoid; *mt*, metapterygoid; *mx*, maxilla; *l*, lacrimal; *op*, opercle; *p*, palatine; *phbr 2-4*, pharyngobranchials 2-4; *pmx*, premaxilla; *pro*, preopercle; *q*, quadrate; *r. br*, branchiostegal rays; *so*, subopercle; *sy*, symplectic; *ur*, urohyal; *v. hh*, ventral hypohyal.

considered plesiomorphies (Voskoboinikova, 1988a, 1988b; Andriashev & al., 1989).

However, unlike *P. breviceps*, *A. dewitti* has no hook-like process of the hyomandibular, that can be considered a plesiomorphic condition. Skora (1995) noted the presence of numerous spines on the singulars of *A. dewitti*.

The structure of the skeleton of the gill arches of *A. dewitti* is more similar to that of *G. acuticeps* in the usual (for dragonfish) triangular shape of the hypobranchial 3, presence of the cartilaginous basibranchial 2 (considered as synapomorphy: Iwami, 1985; Balushkin & Voskoboinikova, 1995), and roundish shape of the cartilaginous basibranchial 4.

Pectoral girdle (Fig. 3a). The pectoral girdle of *A. dewitti* has the same structure as in *P. breviceps*, except for the long spine-like dorsal process of the cleithrum being level with its dorsal posterior lobe (Table 1). The radials of *A. dewitti* are rather large, about half of the coracoid length. The scapular foramen is small and has two sharp triangular notches in the scapula and coracoid. There are no interradial foramina.

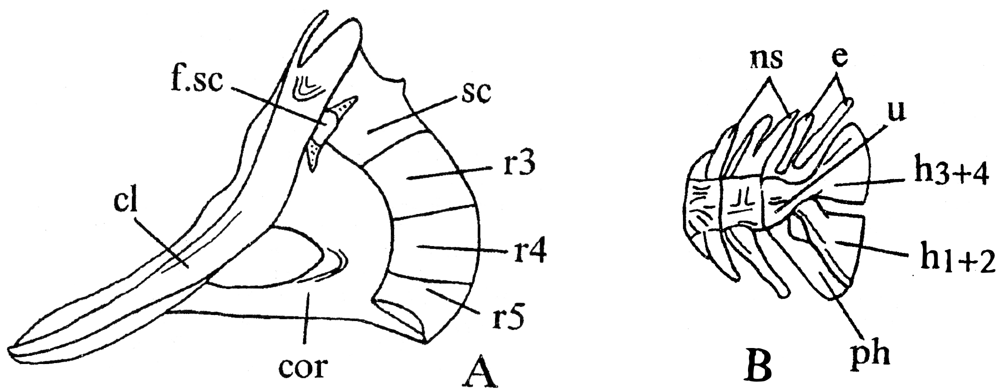

Fig. 3. Pectoral girdle (A) and caudal skeleton (B) of *Acanthodraco dewitti*. *cl*, cleithrum; *cor*, coracoid; *e*, epurals; *f. sc*, scapular foramen; *h*, hypural; *ns*, neural spine; *ph*, parhypural; *r*, radial; *sc*, scapula; *ur*, urostyle.

Axial and caudal skeleton (Fig. 3b). As other gymnodraconins, *A. dewitti* has a small number of vertebrae (16 +32 = 48). The structure of the caudal skeleton of *A. dewitti* is very similar to that of *P. breviceps* and *G. acuticeps*: two hypurals of which hypaxial (1+2) is free and epaxial (3+4) fused with the urostyle. There is no hypural 5. Two neural arches are situated on the first and second preural centra. Andriashev & al. (1983) noted that the structure of the caudal skeleton in the gymnodraconins is obviously advanced compared to skeletons of other bathydraconids.

Discussion

Examination of the osteological structure of *Acanthodraco dewitti* shows that the genus is clearly different from two other gymnodraconin genera not only in the external morphological characters, but also in a number of osteological characters, such as the separated lateral ethmoids, presence of the hook-like ridge of the sphenotic, separation of the intercalar from the prootic, lack of two infraorbitals, and presence of the cartilaginous basibranchial 2.

In most osteological characters, while plesiomorphic, *Acanthodraco* is similar to *Psilodraco*. These two genera are joined by one synapomorphic character only: the lack of the infraorbitals 2 and 3. We consider this character as quite significant because it occurs very rarely among the notothenioids. *Acanthodraco* and *Gymnodraco* also have common characters, such as the separation of the lateral ethmoids by the cartilaginous bar and presence of the cartilaginous basibranchial 2. Except *Psilodraco*, all the bathydraconids have separated lateral ethmoids (Iwami, 1985; Andriashev & al., 1989), and *Parachaenichthys* and *Cygnodraco* have the cartilaginous basibranchial (Balushkin & Voskoboinikova, 1995). So, we consider these two characters as parallelisms in the evolution of *Acanthodraco* and *Gymnodraco*. It is possible that *Acanthodraco* and *Psilodraco* have common origin and both genera acquired similar modification in the structure of the head seismosensory system. Later evolution of *Psilodraco* went in direction of further complication of the seismosensory system of body (Voskoboinikova & Balushkin, 1988), and *Acanthodraco* obtained some advanced osteological characters. The main trend in evolution of *Gymnodraco* was probably the modification of the skeleton structure. It is possible that the evolution of the osteological characters of *Acanthodraco* and *Gymnodraco* went parallel and followed main trend of evolution in the bathydraconids.

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