

## The postcranial skeleton of the benthophiline gobiids *Anatirostrum* and *Benthophilus* (Teleostei: Gobiidae)

Harald AHNELT

*Institute of Zoology, Department of Comparative Anatomy and Morphology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria; e-mail: harald.ahnelt@univie.ac.at*

Received 9 September 2002; Accepted 31 January 2003

**Abstract.** The postcranial skeleton of the Ponto-Caspian endemic benthophilines *Anatirostrum* and *Benthophilus* show unique specializations within gobioid fishes. Precaudal and caudal vertebrae are reduced in numbers and the dorsal pterygiophore insertion pattern is modified. Pterygiophores, which support no spine or segmented fin ray, are present in the skeletons at the rear of the first dorsal fin and at the second dorsal fin origin. Because of the low number of vertebrae the second dorsal and anal fin pterygiophores of *Anatirostrum* and *Benthophilus* are displaced anteriorly. The pterygiophores that support the first spine of these two median fins are positioned opposite to each other.

**Key words:** Ponto-Caspian, Gobiidae, *Anatirostrum*, *Benthophilus*, systematics, osteology, vertebrae, unpaired fins

### Introduction

The Caspian genus *Anatirostrum* Iljin, 1930 and the Ponto-Caspian genus *Benthophilus* Eichwald, 1831 share unique osteological features within endemic Ponto-Caspian gobiids (Ahnelt et al. 2000). These endemic gobiid fishes are of ‘Sarmatic’ origin and characterized by specializations, e.g. loss of swimbladder, modified ctenoid scales and increased total number of vertebrae (Iljin 1930, Kryzhanovskii & Ptschelina 1941, Berg 1949).

*Anatirostrum* and *Benthophilus* are here considered as members of the genus-group (tribe) benthophiline. This genus-group comprises the following genera: *Asra* Iljin, 1941, *Anatirostrum*, *Benthophiloides* Beling & Iljin, 1927, *Benthophilus* and *Caspiosoma* Iljin, 1927. The osteology of *Asra*, *Benthophiloides* and *Caspiosoma* (with *Anatirostrum* and *Benthophilus* united as Benthophilinae by Iljin (1930)), is incompletely known and not considered in this study. Iljin (1930) did not include *Caspiosoma* in the Benthophilinae, but Pynchuk (1980) demonstrated the close relationship of this genus to *Asra* and *Benthophiloides*.

Except for Miller (1973), the benthophiline gobiids have not been considered in modern classifications of gobioid fishes (Hoese 1984, Birdsong et al. 1988, Harrison 1989, Hoese & Gill 1993, Pezold 1993, Simonovic 1999, Akihito et al. 2000). Miller (1973) noted that the bony tubercles and granules, which replace the scales in *Anatirostrum* and *Benthophilus*, are specializations, and that the skeleton of *Benthophilus* is like that of the Gobiinae. Pezold (1993) proposed a monophyletic Gobiinae based on the supraorbital canal of the lateral line system and on features of the postcranial skeleton, for example, pterygiophore formula, total number of vertebrae and number of prehaemal pterygiophores. *Anatirostrum* and *Benthophilus*, both

not considered in Pezold's (1993) classification, are characterized by the absence of head canals of the lateral line system, pterygiophore formula distinctly differing from those of general Gobiinae, a higher number of vertebrae and a lower number of prehaemal pterygiophores. The loss of the head canals of the lateral line system is a derived character within the Gobiidae and is known from many taxa of Gobiinae. In the following I do not refer to this feature, discussed by Ahnelt et al. (2000).

Ahnelt et al. (2000) described the postcranial osteology of *Anatirostrum* and *Benthophilus*, but did not assign these genera to a subfamily of Gobiidae *sensu* Pezold (1993).

## Materials and Methods

The pterygiophore formula (first dorsal fin pterygiophore insertion pattern) generally follows Birdsong et al. (1988). The first digit indicates the interneural space into which the first pterygiophore of the first dorsal fin inserts, the last indicates the interneural space between the last pterygiophore of the first dorsal fin and the first pterygiophore of the second dorsal fin. Pterygiophores which support no spine or segmented fin ray are indicated by superscript asterisks. A pterygiophore formula starting with 3-22 indicates four pterygiophores, two inserting between the neural spines of the third and fourth vertebrae, two between the neural spines of the fourth and fifth vertebrae. A pterygiophore formula starting with 3-22(11\*) indicates the same position of the first four pterygiophores as above, but, in parentheses, that the second pterygiophore of those between the neural spines of the fourth and fifth vertebrae is not supporting a spine. The first caudal vertebra is defined as the first vertebra with a closed haemal arch (parapophyses fused at their tips) and haemal spine.

HS, haemal spine; NS, neural spine; PT, pterygiophore; VT, vertebra.

The description of the osteological features of *Anatirostrum* is based on X-rays, those of the other Gobiidae on X-rays and cleared and stained specimens.

Institutions: CAS, California Academy of Sciences, San Francisco; CMNFI and NMC, Canadian Museum of Nature, Ottawa; IZUW, Institut für Zoologie der Universität Wien, Vienna; ZISP, Zoological Institute, St. Petersburg.

The following specimens were examined (collection number, number of specimens, sex, SL in mm, sampling site, date, collector). The standard length from X-rays is given if specimens are not bent. The sex was determined by the shape of the urogenital papilla and is indicated except for specimens from radiographs.

*Anatirostrum profundorum* (Berg, 1927): CMNFI 1999-0023, 4 females, 76.1 – 79.1, Caspian Sea, Iran, off Astara, 20-21 Feb. 1997, leg. A. Abdoli, M. Naderi. ZISP 23134, 14 juveniles, 23.1 – 31.7, Caspian Sea, Turkmenistan, 22 April 1904, leg. N.M. Knipovich, syntypes of *Benthophilus profundorum*. For information on the type status see Ahnelt et al. (2000).

*Benthophilus* sp.: NMC uncatalogued, 1 specimen, Caspian Sea, Iran, 10 July 1996, A. Abdoli, from X-ray. IZUW uncatalogued, 2 specimens, 1 male, 71.3, 1 female, 59.7, otherwise no data, cleared and stained.

*Benthophilus macrocephalus* (Pallas, 1788): NMC 70-543, 1 large specimen out of two, Caspian Sea, Iran, Gilan, near Bandar Anzali, 13 March 1962, leg. V.D. Vladykov, from X-ray. NMC 70-544, 2 specimens, 20 Mar. 1962, otherwise same data, from X-rays.

*Benthophilus stellatus* (Sauvage, 1874): CAS 27893, six specimens, 41.7 – 53.5, Romania, Danube River drainage, Lake Crapina, floodplain of the Danube near Vacareni, NNE from Macin, Dobrogea, 03 Dec. 1968, leg. P. Banarescu, from X-rays. CAS 52847, 2 specimens, 1 male, 51.3, 1 female, 46.7, same data, cleared and stained.

*Benthophilus stellatus leobergi* Iljin in Berg, 1949: NMC 71-326A, 1 specimen, Caspian Sea, Iran, Gilan, near Bandar Anzali, 10 April 1962, leg. V.D. Vladykov, from X-ray. NMC 93-0105, 1 specimen, Caspian Sea, Iran, Golestan, Gorgan Bay, Feb. 1987, leg. B.H. Kiabi, from X-ray.

## Comparative material

Number of vertebrae, insertion of first pterygiophore of second dorsal fin between neural spines of the seventh and eighth vertebrae, and alignment of first anal-fin pterygiophore with pterygiophores of second dorsal fin (from radiographs and from cleared and stained specimens).

Northeastern Atlantic and Mediterranean species: *Corcyrogobius liechtensteini* (Kolombatovic, 1891), IZUW uncatalogued (4 spms); *Didogobius splechnai* Ahnelt & Patzner, 1995: IZUW uncatalogued (1 spm); *Gammogobius steinitzi* Bath, 1971: IZUW uncatalogued (3 spms); *Gobius bucchichi* Steindachner, 1870: IZUW uncatalogued (1 spm); *Gobius cobitis* Pallas, 1814: NMW 93733, IZUW uncatalogued (2 spms); *Gobius cruentatus* Gmelin, 1789: CAS 101983 (2 spms); *Gobius niger* Linnaeus, 1758: CAS 101970, NMW 93778 (4 spms); *Gobius paganellus* Linnaeus, 1758: IZUW uncatalogued (2 spms); *Thorogobius ephippiatus* (Lowe, 1839): CAS 62428 (1 spm); *Zebrus zebrus* (Risso, 1826): IZUW uncatalogued (1 spm); *Zosterisessor ophiocephalus* (Pallas, 1814): CAS 58326, IZUW uncatalogued (4 spms).

Ponto-Caspian species: *Neogobius* sp. (*cephalargoides*? Pinchuk, 1976), CAS 62205 (3 specimens); *Neogobius fluviatilis* (Pallas, 1814): CAS 62211, IZUW uncatalogued (5 spms.); *Neogobius gymnotrachelus* (Kessler, 1857): CAS 22973, CAS 62210, IZUW uncatalogued (7 spms); *Neogobius kessleri* (Günther, 1861): CAS 23423, CAS 62208, IZUW uncatalogued (28 spms); *Neogobius melanostomus* (Pallas, 1814): CAS 62209, IZUW uncatalogued (5 spms.), *Neogobius ratan* (Nordmann, 1840): CAS 162206 (1 spm); *Neogobius syrman* (Nordmann, 1840): CAS 23433, CAS 62207 (4 spms).

## Results

### Vertebrae

*Anatirostrum profundorum*: 29 vertebrae (including urostyle); 9 precaudal and 20 caudal.

*Benthophilus* sp.: 29–30 vertebrae (including urostyle) (29: 2, 30: 1); 10 precaudal and 19–20 caudal (19: 2, 20: 1).

*Benthophilus macrocephalus*: 27 - 28 vertebrae (including urostyle) (27: 2, 28: 1); 9 precaudal and 18–19 caudal (18: 2, 19: 1).

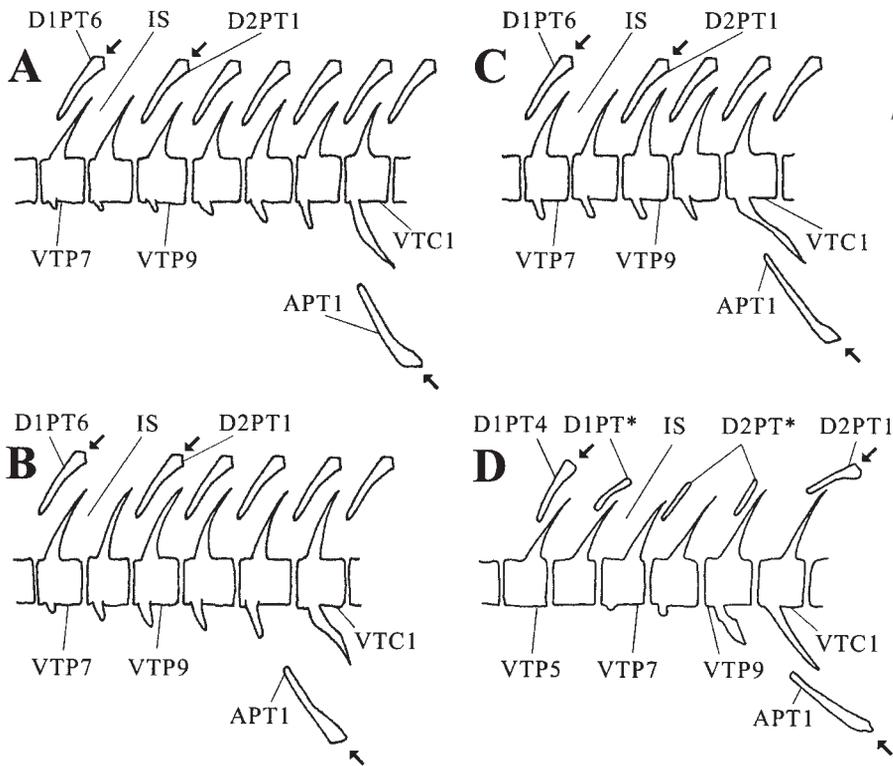
*Benthophilus stellatus*: 28–30 vertebrae (including urostyle) (28: 2, 29: 5, 30: 1); 9 precaudal and 19–21 caudal (19: 2, 20: 5, 21: 1).

*Benthophilus stellatus leobergi*: 29 vertebrae (including urostyle); 10 precaudal and 19 caudal.

## Dorsal and ventral pterygiophores

*Anatirostrum profundorum*: Three pterygiophores that support no spine or fin ray developed between the two dorsal fins. Pterygiophore formula 3-221\*0; anterior three pterygiophores of second dorsal fin 1\*1\*1, with third PT supporting spine at origin of second dorsal fin; free interneural space between the last and first pterygiophore of the first and second dorsal fins between neural spines of VT6 and VT7. A single (first) PT of anal fin (prehaemal pterygiophore) inserts between parapophysis of last precaudal (VT9) and haemal spine of first caudal vertebra (VTC1); it lines up with the third PT of the second dorsal fin, the first which supports a fin ray.

*Benthophilus* sp.: Four pterygiophores which support no spine or fin ray are developed between the first and second dorsal fins. Pterygiophore formula 3-221\*0 (n=1) and 3-22(11\*)1\*0 (n=2); anterior pterygiophores of second dorsal fin 1\*1\*1\*1 (n=1) and



**Fig. 1.** Stylized anterior vertebrae and fin pterygiophores in **A:** *Neogobius melanostomus*, female, 59.5 mm SL, Romania, Danube; **B:** *Gobius bucchichi*, male, 35.2 mm SL, Spain, Balearic Islands; **C:** *Zebrus zebrus*, male, 19.4 mm SL, Spain, Balearic Islands; **D:** *Anatirostrum profundorum* (from X-ray), Iran, off Astara. APT1, first pterygiophore of the anal fin; D1PT4, D1PT6, fourth and sixth pterygiophore of the first dorsal fin; D1PT\*, D2PT\*, remnants of pterygiophores of the first and second dorsal fins which support no spine or segmented fin-ray; D2PT1, first pterygiophore of the second dorsal fin which supports the spine; IS, interneural space between pterygiophores of first and second dorsal fins; VTC1, first caudal vertebra; VTP5, VTP9, fifth and ninth precaudal vertebra. Arrows indicate position of last spine of the first dorsal fin and spines of the second dorsal and anal fins. Note differences in alignment of APT1 with D2PT, position of VTP9 to VTC1 and IS between neural spines of VTP7 – VTP8 (**A - C**) or between neural spines of VTP6 – VTP7 (**D**).

1\*1\*1\*02 (n=2), with fourth PT supporting spine at origin of second dorsal fin; free interneural space between the last and first pterygiophore of the first and second dorsal fins between neural spines of VT6 and VT7; first spineless PT of second dorsal fin between neural spines of VT7 and VT8; first PT of second dorsal fin which supports a spine together with the following PT in the interneural space between VT11 and VT12 (n= 2) instead between VT10 and VT11 (n=1) , thus an additional (atypical) free interneural space anteriorly to the origin of the second dorsal fin is present in two specimens. A single (first) PT of anal fin extends before first haemal spine (VT11), lining up with first PT of second dorsal fin which supports a spine (n=1) or with free interneural space between neural spines of VT10 and VT11 (n=2).

*Benthophilus macrocephalus*: Four PT which support no spine or fin ray are developed between first and second dorsal fins. Pterygiophore formula 3-22(11\*)1\*0; anterior pterygiophores of second dorsal fin 1\*1\*1 (n = 2) and 1\* 1\*02 (n = 1), with third PT supporting spine at origin of second dorsal fin; free interneural space of the first and second dorsal fins between neural spines of VT6 and VT7; first spineless PT of second dorsal fin between neural spines of VT7 and VT8; first PT supporting the spine of second dorsal fin between neural spines of VT10 and VT11 (n =1) or together with second PT in the interneural space between VT11 and VT12 (n = 1), thus an additional (atypical) free interneural space anteriorly to the origin of the second dorsal fin is present. A single (first) PT of anal fin extends before first haemal spine (VT10); it lines up with the first PT of the second dorsal fin which supports a spine between the neural spines of VT9 and VT10 (not between VT10 and VT11 as erroneously mentioned in A h n e l t et al. (2000)) in two specimens and with the free interneural space between VT9 and VT10 in one specimen.

*Benthophilus stellatus*: Three to five PT which support no spine or fin ray are developed between the first and second dorsal fins. Pterygiophore formula 3-221\*0 (n = 3) and 3-22(11\*)1\*0 (n = 4); anterior three pterygiophores of second dorsal fin 1\*1\*1 (n = 3) and 1\*1\*1\*1 (n = 4), with third or fourth PT supporting spine at origin of second dorsal fin; free interneural space between neural spines of VT6 and VT7; free interneural space between the last and first pterygiophore of the first and second dorsal fins between neural spines of VT6 and VT7; first spineless PT of second dorsal fin between VT7 and VT8. One (first) PT of anal fin extends before first haemal spine (VT10); it lines up with the first PT of the second dorsal fin which supports a spine (n = 3) and with the last spineless PT (n = 4).

*Benthophilus stellatus leobergi*: Four PT which support no spine or fin ray are developed between first and second dorsal fins. Pterygiophore formula 3-221\*0 (n = 1); anterior pterygiophores of second dorsal fin 1\*1\*1\* 02 (n = 1); free interneural space between the last and first pterygiophore of the first and second dorsal fins between neural spines of VT6 and VT7; first PT of second dorsal fin which supports a spine together with the following PT in the interneural space between VT11 and VT12 instead between VT10 and VT11, thus an additional (atypical) interneural space anteriorly to the origin of the second dorsal fin without PT (NMC-71-326A); anterior series of PT in the second specimen not determinable, but three PT not supporting a spine or fin ray anterior to origin of second dorsal fin, last in the interneural space between neural spines of VT9 and VT10 (1\*1\*1\*1); free interneural space between first and second dorsal fin between neural spines of VT6 and VT7. A single (first) PT of anal fin extends before first haemal spine (VT11); it lines up with the free interneural space immediately anterior to the origin of D2 or with the first PT of the second dorsal fin which supports a spine.

## Discussion

According to Ahnelt et al. (2000) *Anatirostrum* Iljin, 1930 and *Benthophilus* Eichwald, 1831 are characterized by postcranial skeletons with, (i) dorsal pterygiophore formula 3-221\*01\*1\* or 3-221\*01\*1\*1\*(mode) (PT without dorsal fin ray marked by asterisk), (ii) no free interneural space between the pterygiophores of the first and second dorsal fins, (iii) 9 precaudal vertebrae (mode), (iv) 19-20 caudal vertebrae, (v) first PT of the second dorsal fin inserting between neural spines of VT9 and VT10 or VT10 and VT11 (mode) and (vi) first anal PT lining up with the first PT of the second dorsal fin. The derived pterygiophore formula of *Anatirostrum* and *Benthophilus* was seen in part as a result of the backward shift of the second dorsal fin by these authors.

This backward shift of the second dorsal fin in *Anatirostrum* and *Benthophilus* seemingly only concerns the external fin elements (fin spine and segmented fin rays). In many gobioids and especially in gobies from the northeastern Atlantic, the Mediterranean and the Ponto-Caspian regions, the first PT of the second dorsal fin is positioned two vertebrae or more anterior to the first PT of the anal fin (for example Hoesse & Gill 1993, McKay & Miller 1997, Scsepka et al. 1999, Akihito et al. 2000, Ahnelt & Duchkowsch 2003, Murdy & Shibukawa 2002) (Fig. 1). Generally these pterygiophores also support the spines of the second dorsal and the anal fins. In *Anatirostrum* and *Benthophilus* these PT which support the spines of the second dorsal and the anal fins are positioned opposite to each other. But the internal elements (i.e. the spineless pterygiophores) of the second dorsal fin have not been reduced completely and, still originate two vertebrae anterior to the first PT of the anal fin (Fig. 1). These pterygiophores anterior to the rays of the second dorsal fin do not support a fin ray and seemingly are the remnants of a former more anteriorly originating second dorsal fin. This implicates that in *Anatirostrum* and *Benthophilus* (i) the dorsal PT formula has to be changed from 3-221\*01\*1\* to 3-221\*0 or 3-22(11\*)1\*0, (ii) a single free interneural space between the (spineless) pterygiophores of the first and second dorsal fins is present and (iii) the PT formula for the second dorsal fin, unique for gobiids of the Atlantic, the Mediterranean and Ponto-Caspian regions, starts with two or three PT supporting no fin ray (1\*1\* or 1\*1\*1\*).

In addition precaudal vertebrae anterior to VT7 must have been lost. This would explain why: (i) only five pterygiophores are developed in the first dorsal fin instead the plesiomorphic six, with the posteriormost lost; (ii) the origins of the second dorsal and the anal fins are displaced anteriorly, with the first spineless PT of second dorsal fin between neural spines of VT7 and VT8 instead between VT8 and VT9, and with the first PT of the anal fin positioned anterior to the haemal spine of VT10 or VT11 instead e.g. VT11, VT12 or VT13; (iii) a single interneural space without a PT is occurring between the pterygiophores of the two dorsal fins (Fig. 1).

This single interneural space is only explainable if at least one precaudal vertebra has been lost. Such a single interneural gap is characteristic for gobiines (Hoesse & Gill 1993). It occurs between the neural spines of VT7 and VT8 in gobies of the northeastern Atlantic, the Mediterranean and the Ponto-Caspian with the plesiomorphic 10 or more precaudal vertebrae, with the plesiomorphic six spines in the first dorsal fin and with the free interneural space between the pterygiophores of the two dorsal fins single and not secondarily increased (Ahnelt & Duchkowsch 2003, Ahnelt unpublished). The loss of the sixth PT of the first dorsal fin would result in a second gap. But with the

reduction of a precaudal vertebra, likely the vertebra associated with the lost sixth PT of the first dorsal fin, a single interneural space lacking a PT would result.

If one accepts the benthophilines and neogobiines as monophyletic sister groups, then benthophiline gobies represent the derived group with loss of the head canals of the lateral line system, transverse interorbital rows of free neuromasts, a lower vertebral mode, and modified ctenoid scales or naked. *Asra*, *Benthophiloides* and *Caspiosoma* differ from *Anatirostrum* and *Benthophilus* in having a higher number of spines in the first dorsal fin and, consequently, must also differ in features of the dorsal pterygiophores and the dorsal pterygiophore formula. However the osteology of these benthophiline gobiids is unknown.

The other benthophiline gobiids, *Anatirostrum* and *Benthophilus*, are apomorphic compared with neogobiines in the following characters (plesiomorphic condition in parentheses): (i) first dorsal fin with 3-4 spines and 5 pterygiophores (6 spines and 6 pterygiophores), (ii) head canals of the lateral line system absent (head canals present), (iii) transverse interorbital series of free neuromasts (no free neuromasts in interorbital region), (iv) bony scutes and granules, adult males naked (typical ctenoid scales), (v) lower number of vertebrae, 9-10 precaudal + 19-20 caudal (12-13 precaudal + 21-22 caudal vertebrae), (vi) 2-3 pterygiophores supporting no spines or fin rays between first and second dorsal fins (all pterygiophores supporting spines), (vii) dorsal pterygiophore formula 3-221\*0 (mode) (3-22110 (mode)), (viii) first PT of the second dorsal fin preceded by two or three spineless pterygiophores with a PT starting sequence of 01\*1\*1 or 01\*1\*1\*1 (first PT of the second dorsal fin not preceded by spineless pterygiophores with a PT starting sequence of 01), (ix) first PT of second dorsal fin inserting between neural spines of posteriormost precaudal (VT9-VT10) and first caudal (VT10-VT11) vertebra (inserting between neural spines of VT8 and VT9, thus at least two vertebrae anterior of the first caudal vertebra), (x) one anal fin (prehaemal) pterygiophore, aligned with first PT of second dorsal fin (2-3 anal pterygiophores aligned with fourth or fifth PT of second dorsal fin), and (xi) caudal skeleton with epural and haemal spine of last vertebra broader than long at their distal margins (epural and haemal spine of last vertebra longer than broad) (A h n e l t et al. 2000).

Another feature that possibly separates benthophilines from neogobiines is the number of longitudinal neuromast rows on the caudal fin. Three longitudinal rows are present on the caudal fin of neogobiines but only two, the dorsal and median rows, are present in *Anatirostrum* and *Benthophilus* (A h n e l t et al. 2000, A h n e l t & D u c h k o w i t s c h 2001). The topography of the neuromasts on the caudal fin of the remaining benthophilines *Asra*, *Benthophiloides*, and *Caspiosoma* is unknown. If this feature, two longitudinal rows of neuromasts on the caudal fin, is consistent in all benthophilines, it should be added to the above mentioned list of differences between these two genus-groups.

Based on the above mentioned features of the lateral line system and the postcranial osteology, I assign *Anatirostrum* and *Benthophilus* to the Gobiinae sensu P e z o l d (1993).

*Anatirostrum* and *Benthophilus* are highly specialized gobiid fishes (M i l l e r 1973) which are seemingly derived from a common ancestor (A h n e l t et al. 2000). Because of their specializations (for example the modified lateral line system and bony scutes and granules that cover the trunk and head) a close relationship to neogobiines or a more basic gobiine stock is not obvious.

About 12 million years ago (Middle Miocene), when the Paratethys was a sea with reduced salinity and high endemism (R ö g l 1998), an ancestral Ponto-Caspian endemic neogobiine stock seemingly differentiated from an Atlantic-Mediterranean gobiine stock

(Miller 1990, McKay & Miller 1991). This scenario agrees with the findings of Dillon & Stepien (2001) who, based on mitochondrial DNA, suggest that the Ponto-Caspian endemic neogobiine stock evolved from an ancestral *Gobius* lineage during the isolation of the Paratethys basins in Middle Miocene.

If an ancestor of *Anatirostrum* and *Benthophilus* developed from such a basic gobiid stock characterized by 10-11 precaudal and 16-17 caudal vertebrae this would imply the following changes in the postcranial skeleton: (i) reduction to 9-10 precaudal vertebrae, with loss of none, one, or two vertebrae, (ii) reduction from 6 pterygiophores to 5 in the first dorsal fin and (iii) increase of caudal vertebrae to 19-20. This involves a combination of the loss of precaudal vertebrae and a simultaneous increase of caudal vertebrae.

If an ancestor of *Anatirostrum* and *Benthophilus* developed from a neogobiine stock characterized by 12-13 precaudal and 21 caudal vertebrae this would imply: (i) reduction from 12-13 to 9-10 precaudal vertebrae, with loss of 2-3 vertebrae, (ii) reduction from 6 pterygiophores to 5 in the first dorsal fin, and (iii) loss of 1 or 2 caudal vertebrae resulting in the alignment up of the first anal PT (= first which supports the fin spine) with the third PT of the second dorsal fin. This involves the simultaneous loss of precaudal and caudal vertebrae.

From features of the postcranial skeleton a closer relationship of *Anatirostrum* and *Benthophilus* to the neogobiine stock appears more likely than to a basic gobiine stock. Testing this hypothesis must await information on the osteology of *Asra*, *Benthophiloides* and *Caspiosoma*, which display higher numbers of fin rays. Consequently the dorsal pterygiophore formula, the pterygiophore insertion pattern, and possibly the number of vertebrae of these genera may differ from those of *Anatirostrum* and *Benthophilus*.

#### Acknowledgements

For providing material and radiographs I thank W. Eschmeyer, T. Iwamoto and D. Catania (California Academy of Sciences, San Francisco), B.W. Coad (Canadian Museum of Nature, Ottawa) and N. Bogutskaya, A. Naseka (Zoological Institute, St. Petersburg). I am indebted to V.G. Springer (National Museum of Natural History, Washington) for commenting on an earlier version of the manuscript.

#### LITERATURE

- AHNELT H., ABDOLI A., NADERI M. & COAD B.W. 2000: *Anatirostrum profundorum*: a rare deep-water gobiid species from the Caspian Sea. *Cybius* 24: 139–159.
- AHNELT H. & DUCHKOWITSCH M. 2001: The lateral line system of two Ponto-Caspian gobiid species (Gobiidae, Teleostei): a comparison. *Folia Zool.* 50: 217–230.
- AHNELT H. & DUCHKOWITSCH M. 2003: The postcranial skeleton of *Proterorhinus marmoratus* with remarks on the relationships of the genus *Proterorhinus* (Teleostei: Gobiidae). *J. Nat. Hist.* (in press).
- AKIHITO IWATA A., KOBAYASHI T., IKEO K., IMANISHI T., ONO H., UMEHARA Y., HAMAMATSU C., SUGIYAMA K., IKEDA Y., SAKAMOTO K., FUMIHITO A., OHNO S. & GOJOBORO T. 2000: Evolutionary aspects of gobioid fishes based upon a phylogenetic analysis of mitochondrial *b* genes. *Gene* 259: 5–15.
- BERG L.S. 1949: Freshwater fishes of the U.S.S.R. and adjacent countries. Volume 3. *IzdateIstvo Akademii Nauk SSSR, Moscow: 929–1381* (in Russian, translated by the Israel Program for Scientific Translations, Jerusalem, 1965, p. 921–1381).
- BIRDSONG R.S., MURDY E.O. & PEZOLD F.L. 1988: A study of the vertebral column and median fin osteology in gobiid fishes with comments on gobioid relationships. *Bull. Mar. Sci.* 42: 174–214.
- DILLON A.K. & STEPIEN C.A. 2001: Genetic and biogeographic relationships of the invasive round (*Neogobius melanostomus*) and tubenose (*Proterorhinus marmoratus*) gobies in the Great Lakes versus Eurasian populations. *J. Great Lakes Res.* 27: 267–280.

- HARRISON I.J. 1989: Specialization of the gobioid palatoquadrate complex and its relevance to gobioid systematics. *J. Nat. Hist.* 23: 325–353.
- HOESE D.F. 1984: Gobioidae: relationships. In: Moser H.G., Richards W.J., Cohen D.M., Fahay M.P., Kendall A.W., Jr. & Richardson S.L. (eds), Ontogeny and systematics of fishes. *Special Publications No. 1, American Society of Ichthyology and Herpetology, Allen Press, Lawrence*: 558–591.
- HOESE D.F. & GILL A.C. 1993: Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidae). *Bull. Mar. Sci.* 52: 415–440.
- ILJIN B.S. 1930: Le système des Gobiidés. *Trab. Inst. Espan. Oceanogr., Madrid* 2: 1–63.
- KRYZHANOVSKII S.G. & PTSHELINA Z.M. 1941: Über das System der Gobiidae. *Zool. Zh.*, 20: 446–455 (in Russian with German summary).
- McKAY S.I. & MILLER P.J. 1991: Isozym criteria in the testing of phyletic relationships between species of *Gobius* and related eastern Atlantic-Mediterranean genera (Teleostei: Gobiidae). *J. Fish Biol.* 39 (Supplement A): 291–299.
- McKAY S.I. & MILLER P.J. 1997: The affinities of European sand gobies (Teleostei: Gobiidae). *J. Nat. Hist.* 31: 1457–1482.
- MILLER P.J. 1973: The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidae) and the classification of gobioid fishes. *J. Zool.* 171: 397–434.
- MILLER P.J. 1990: The endurance of endemism: the Mediterranean freshwater gobies and their prospects for survival. *J. Fish Biol.* 37 (Supplement A): 145–156.
- MURDY E.O. & SHIBUKAWA K. 2002: Redescription of the gobiid fish *Pseudotrypauchen* (Gobiidae: Amblyopinae) and its significance in amblyopine phylogeny. *Mar. Freshwater Res.* 53: 253–258.
- PEZOLD F. 1993: Evidence for a monophyletic gobiinae. *Copeia* 1993(3): 634–643.
- PINCHUK V.I. 1980: The lateral-line system of *Caspiosoma caspium* (Kessler, 1877) and the systematic status of *Asra turcomanus* Iljin, 1941. *J. Fish Biol.* 17: 231–235.
- RÖGL F. 1998: Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien* 99A: 279–310.
- SCSEPKA S., AHNELT H., HERLER J. & HILGERS H. 1999: Morphology of two rare Mediterranean gobiid fishes (Teleostei: Gobiidae). *Cybium* 23: 169–187.
- SIMONOVIC P.D. 1999: Phylogenetic relationships of Ponto-Caspian gobies and their relationship to the Atlantic-Mediterranean Gobiinae. *J. Fish Biol.* 54: 533–555.