

Stratigraphic succession of the Upper Cretaceous fish assemblages of Kras (Slovenia)

Stratigrafsko zaporedje zgornjekrednih ribjih združb Krasa (Slovenia)

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Ključne besede: ribe, zgornja kreda, Komenski in Tomajski apnenec, Dinarska karbonatna platforma, Kras, Tržaško-komenska planota, Slovenija

Abstract

In the paper new finds of Upper Cretaceous fossil fishes from five levels of the Komen and Tomaj limestones of Kras are discussed. The compositions of the fish assemblages are summed up and their precise stratigraphic position in the strata sedimented between the Cenomanian and Lower Campanian is given. About 74% of studied specimens were collected in the Santonian-Campanian Tomaj limestone in the area between Kazlje, Dobravlje and Tomaj and thus they represent a new fish assemblage if compared to the old collections that originate mainly from the Cenomanian beds of the Komen vicinity.

Kratka vsebina

Članek obravnava nove najdbe zgornjekrednih fosilnih rib iz petih nivojev Komenskega in Tomajskega apnenca Krasa. Podana je ocena sestave ribjih združb in njihova stratigrafska lega v plasteh, ki so se sedimentirale med cenomanijem in spodnjim campanijem. Približno 74% raziskanih primerkov je iz santonijsko-campanijskega Tomajskega apnenca med Kazljami, Dobravljami in Tomajem, zato v primerjavi s starimi zbirkami, ki večinoma izvirajo iz cenomanijskih plasti okolice Komna, predstavljajo novo združbo rib.

INTRODUCTION

Many popular articles and longer or shorter treatises on fossil vertebrates from the platy and laminated limestones of the Trieste-Komen plateau have been published. The first written records date from the first half of the nineteenth century (see: Calligaris, 1994, Calligaris et al.,

1994). Gorjanović-Kramberger (1895) in his work *De piscibus fossilibus Comeni, Mrzleci, Lesinae et M. Libanonis et appendix de piscibus oligocaensis ad Tüffer, Sagor et Trifail* described and illustrated for the first time in detail the specimens from Komen. Moreover, particular finds of fossil fishes and reptiles were reported also by some other geologists of the second half of

the nineteenth century. Among them were Heckel (1850, 1856), Steindachner (1860), Kner (1863, 1867), Bassani (1879, 1880), and others. A study on the museum collection of fossil fishes from the vicinity of Komen and Gorica (Gorizia) presently housed in the Museo Civico di Storia Naturale in Trieste (70 specimens) was published by Calligaris (1992). Many specimens of the collection were found as early as the nineteenth or the first half of the twentieth century.

In the nineteenth and beginning of the twentieth century, there were numerous small quarries operating in the Trieste-Komen plateau to acquire limestone slabs for roofing and paving. Therefore, finds of fossil fishes were proportionally frequent. Because of the fish content and shaly appearance of the rock, Gorjanović-Kramberger (1895) introduced the term "ichthyiferous shales" into the scientific literature. He also dealt with the problem of the age of the fish-bearing strata that had been unsolved for decades. He believed that the "shales" of Komen and Mrzlek with their fauna, as well as some other localities of dark shales in Kras, represent contemporaneous sediments of the same

Upper Cretaceous (?Cenomanian) horizon. He concluded that the localities were coeval based on a correlation of these strata with the rudist limestone as well as on their petrographic and faunal similarities.

The exact age and stratigraphic position of the platy and laminated limestones of the Trieste-Komen plateau has not been entirely clear even to later researchers. D'Erasmio (1946) studied the paleontological part of the private Holler collection (it later passed into the possession of the Geological museum of the University of Bologna) describing the fossil fishes from Kobjeglava, Komen, Križ, Mali Dol, Gabrovica, Jablanec, Rubije, Škrbina, Sveto, Tomačevica and Volčji Grad. The described fish-bearing localities stratigraphically encompass strata ranging from the Cenomanian to the Upper Santonian, and possibly even to the Lower Campanian, which means a range of over 10 Ma. between the oldest and youngest finds.

Pleničar (1960) wrote "that the Komen shales are not a stratigraphic horizon but a special facies of the Senonian, Turonian and possibly the Cenomanian and Lower Cretaceous sediments". This statement was later confirmed during the elaboration of

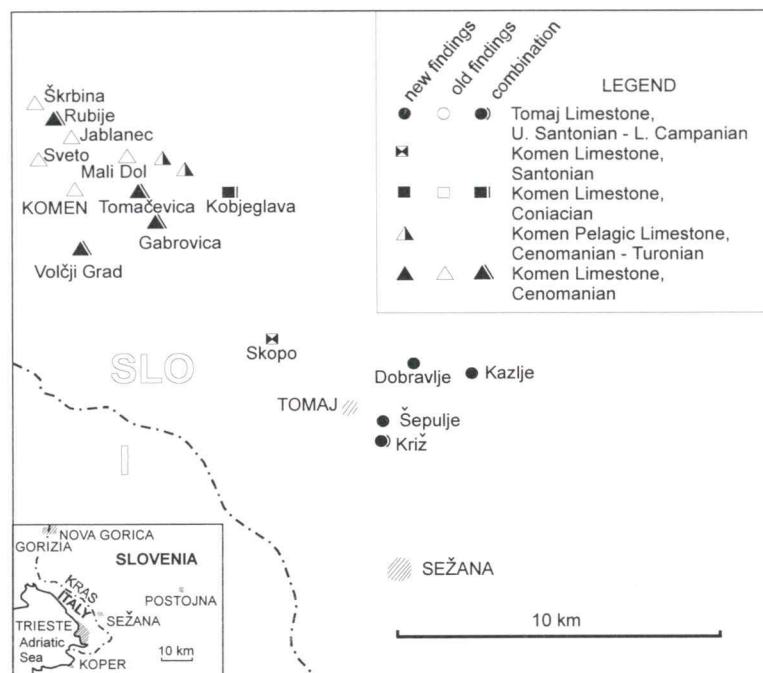


Fig. 1. Geographic sketch map showing distribution of localities with fossil fishes

Sl. 1. Geografska skica s prikazanimi nahajališči fosilnih rib

the Basic Geological Map 1: 100.000, sheet Gorica (Buser, 1968, 1973).

Investigations for the Geological map of the southern part of the Trieste-Komen plateau 1: 50,000 (Jurkovšek et al., 1996) have indicated that more levels of the platy and laminated limestones with chert can be recognized as previously thought, and above all they are in connection with various modes and areas of origin. Parallel to the geological mapping several paleontological studies of macrofossils from these beds were done (Jurkovšek & Kolar-Jurkovšek, 1995). Among them the fossil fishes are frequent. When the studies for the new geological map 1: 50,000 of Kras are finished a detailed revision of all museum specimens of fishes from the Trieste-Komen plateau will be possible in case their exact locality is stated in the museum catalogues.

This paper documents recent finds of fossil fishes, for the most part unpublished until now (Fig. 1). They are stored in the Paleontological collection Jurkovšek at Dol pri Ljubljani (Slovenia) that has been registered with the Ministry of Culture of the Republic of Slovenia and the Natural History Museum of Slovenia in accordance with current legislation.

The topic of this review is not to provide exhaustive descriptions of the whole material, but to sum up the compositions of the fish assemblages through the stratigraphic column of the Trieste-Komen plateau limestones. Special attention has been paid to some groups because the available specimens provide interesting osteological characters (enchodontids for instance), or because their determination has particular interest for understanding of the succession of fish assemblages (indeterminate euteleosts for instance).

STRATIGRAPHIC PART

Kras in a wider geotectonic sense belongs to the Outer Dinarides, but in a strict tectonic sense, it can be defined as the Trieste-Komen plateau (synclorium) or the Komen thrust sheet.

The geological structure of Kras is characterized by prevailing Cretaceous plat-

form carbonates exceeding altogether a thickness of 2000 m. The greater part of central Kras belongs to Cretaceous formations alternating vertically and horizontally, depending upon paleogeographic and paleoecological conditions, and different local and global influences on the sedimentary environment. Among the latter, there were most distinctly the global changes of the sea level and oceanic anoxic events that were variously reflected in different parts of the Dinaric carbonate platform (Gušić & Jelaska, 1990, Jurkovšek et al., 1996).

Special attention during the geological mapping of the new geological map of the Trieste-Komen plateau has been paid to the dark platy and laminated limestones with chert that occur at several horizons within the bedded platform carbonates. Various thick intercalations of these beds occur in seemingly similar lithological form within different formations ranging from the Cenomanian to the Upper Santonian and Lower Campanian respectively.

Based on the studies of depositional environments and mechanisms of the origin of modern marine carbon rich black shales, Arthur and Sageman (1994) summarized that their deposition can take place in five major modern marine environments. Among them, only the areas of "upwelling" and coastal intertidal zones could be connected with the formation of the Upper Cretaceous bituminous limestones of Kras. Various conditions of their origin, such as configuration of the floor, different water depth, relationship to the surrounding seas, vertical oscillation of the water column, and sedimentation have to be taken into consideration. Common characteristics of all levels of bituminous fish-bearing limestones of Kras are thin beds and frequent laminated beds giving a shaly appearance.

The fossil fishes were sampled from five levels of the Komen and Tomaj limestones (Fig. 2).

1. Komen limestone (Cenomanian)

The oldest localities with fishes are in the Cenomanian level of the Komen limestone at Gabrovica, Tomačevica, Rubije and Volčji Grad. These are typical shallow water marine sediments within the intertidal

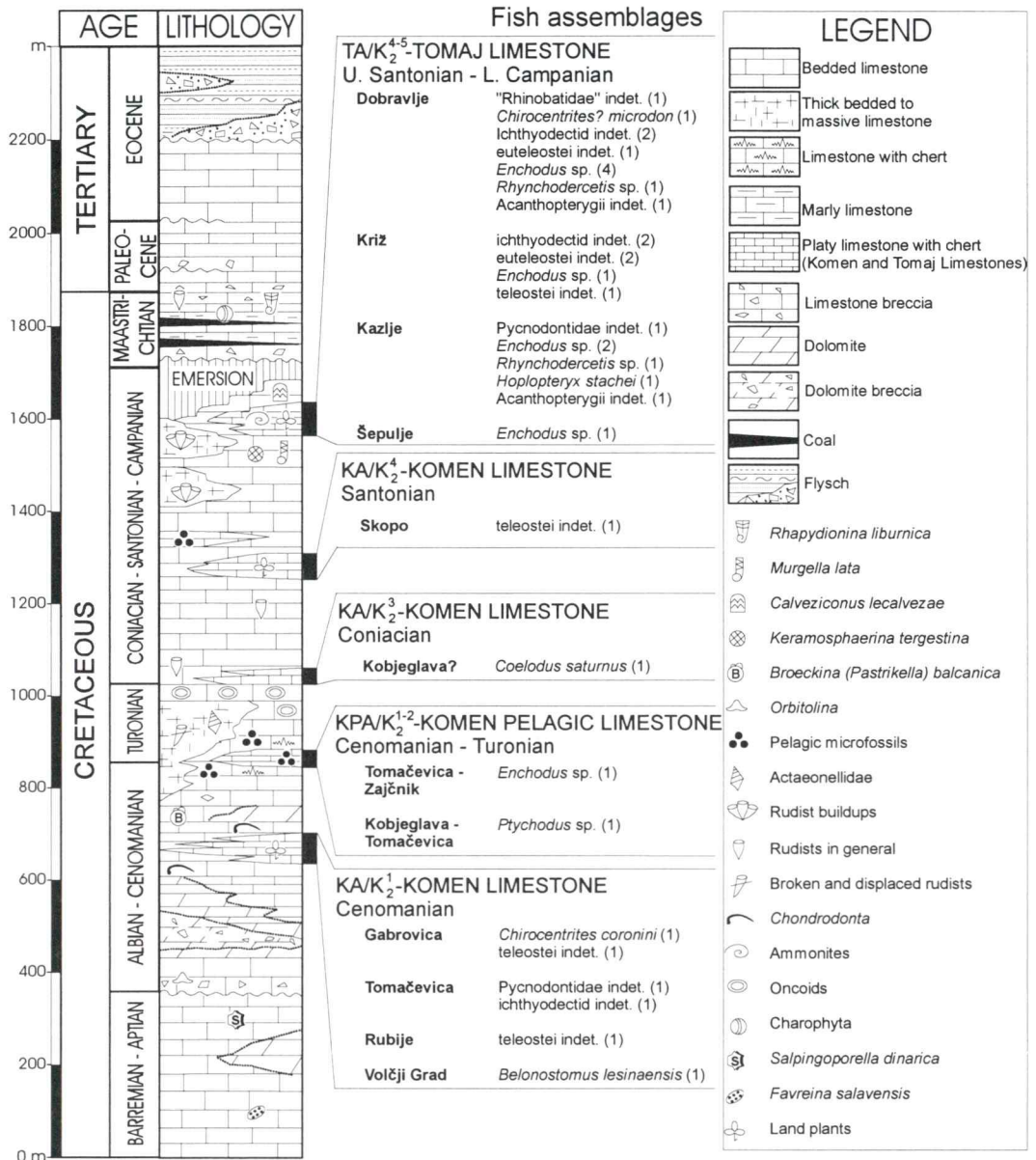


Fig. 2. Stratigraphic column of the Cretaceous beds of the Trieste-Komen plateau with marked positions of localities with fossil fishes

Sl. 2. Stratigrafski stolpec krednih plasti Tržaško-komenske planote z označenimi položaji nahajališč fosilnih rib

and lagoonal environment of low water energy. The sheets of laminite and stromatolite might be locally disrupted and beds of flat pebble conglomerate are present in places. There also occur chert nodules and thinner sheets of chert, dark grey and black

in colour, that is micro- and cryptocrystalline with partly preserved texture of the primary rock. The Cenomanian age of these beds is defined by the *Chondrodonta* levels and the foraminifer *Broeckina (Pastrikella) balcanica* Cherchi, Radoičić & Schroeder.

2. Komen pelagic limestone (Cenomanian - Turonian)

The next is the Cenomanian-Turonian horizon of platy limestone, termed the Komen pelagic limestone in the geological mapping of the Trieste-Komen plateau. The horizon is three to four metres thick and situated within the medium grey micritic limestone. It frequently contains fossil remains of calcitized radiolarians and saccomids next to numerous calcispheres (calcispherical limestone) and pithonellas. The pelagic micritic limestone is a result of the Cenomanian-Turonian eustatic sea level rise (Haque et al., 1987) that caused submergence of numerous platforms and reefs (Arthur & Schlanger, 1979, Jenkyns, 1985, 1991, Weimer, 1988, Hine, 1997), including also the submergence of a greater part of the Dinaric carbonate platform (Gušić et al., 1988, Gušić & Jelaska, 1990, 1993, Davey & Jenkyns, 1999). The calcispherical limestone was deposited in a very quiet environment on the submerged platform. We do not have estimates for the absolute depths during the deposition, but the water should have been deep enough to flood the entire benthic biota associated to the euphotic zone of the carbonate platform.

Carbon rich beds of the Komen surroundings have been often discussed as evidence for the second oceanic event (OAE 2). Based on comparison of facies on the Dinaric-Adriatic platform and conditions in a wider Mediterranean area, Jenkyns (1991) concluded that during the Cenomanian-Turonian there was a particularly thick column of anoxic water. In the Umbria-Marche basin it resulted in the deposition of the Bonarelli Level. OAE 2 consists of more anoxic events and the main level (Bonarelli Level) is preceded by several thinner anoxic levels (Montanari et al., 1995).

Recent researches in Kras have indicated that the main anoxic event was reflected in the deposition of the black platy and laminated Komen pelagic limestone resting within the medium grey bedded micritic limestone with calcispheres. Locally in the laminae of the Komen pelagic limestone the calcispheres and pithonellas are also abundantly represented. The fossil fishes of this horizon were sampled in the

Tomačevica-Zajčnik and Kobjeglava-Tomačevica areas. The macrofossils include also ammonoids.

3. Komen limestone (Coniacian)

The third horizon of the platy and laminated fish-bearing limestones belongs to the Coniacian Komen limestone. It was deposited soon after the global Cenomanian-Turonian pelagic episode. The rapid eustatic sea level drop in the Turonian (Haque et al., 1987) caused the sedimentation of shallow water biomicritic limestone frequently with shrinkage pores, and the oncoid limestone. They are common features exhibited in a wider area and thus representing the beginning of the sedimentation of the Sežana formation. Its lower part is characterized by thinner intercalations of platy, stromatolitic and laminated limestone with fossil fishes.

4. Komen limestone (Santonian)

The fourth sampled horizon is also resting within the Sežana formation. At Skopo village, the four meters thick Santonian section of the Komen limestone is represented by alternating beds of dark biomicritic limestone, laminite, flat pebble conglomerate and stromatolite. Nodules and thin sheets of chert also occur frequently (Ogorelec et al., 1987). Among the fossils there are plant remains (conifers) and fishes.

5. Tomaj limestone (Upper Santonian - Lower Campanian)

The fifth horizon of the platy and laminated limestone with chert, termed the Tomaj limestone is occurring within the Santonian-Campanian Lipica formation. Precise interpretation of the origin of the Tomaj limestone remains not fully understood for the connection with the eustatic sea level rise in this part of the Tethys is still problematic. Based on the presence of allodapic limestones a somewhat deeper depositional environment was presumed by Ogorelec and co-workers (1987), and there are no traces of intertidal conditions (Jurkovšek et al., 1996). A good connection of the sedimentary environment with the open sea is pointed out by pelagic micro- and megafossils with prevailing ammonites with preserved aptychi in body

chambers and their rollmarks, stemless crinoids (Saccocomidae) as well as some other organisms which mean that the water column above the seafloor with anoxic conditions allowed the existence of nektonic and planktonic organisms (Jurkovšek & Kolar-Jurkovšek, 1995, Summesberger et al., 1996a, 1996b, 1999).

At certain levels, a mass mortality (mainly of fishes and saccocomids) is evidenced and it is connected with mixing of well stratified water in a lagoon. Based on current knowledge, a strong pelagic influence in the Tomaj limestone can be linked also to the sea level rise and the second pelagic episode on the Dinaric carbonate platform during the Late Santonian-Campanian (Gušić & Jelaska, 1990, Kolar-Jurkovšek et al., 1996).

The fossil assemblage of the Tomaj limestone is characterized by marine organisms and also the presence of an abundant macroflora (Dobruskina et al., 1999) derived from the land that as early as the Late Santonian began to rise south of the Tomaj lagoon (Pleničar & Jurkovšek, 1997a, 1997b). At Dobravlje, Kazlje, Križ and Šepulje numerous fish specimens were collected. The Upper Santonian to Lower Campanian age of the main horizon of the Tomaj limestone with fishes is in a wider area indicated by the abundant Late Santonian foraminifera *Murgella lata* (Luperto Sinni) in the underlying strata or laterally in the rudist beds corresponding to its lower part, and by the Campanian species *Calveziconus lecalvezae* Caus & Cornella in overlying beds (Šribar, 1995).

FOSSILIZATION

Fossil fishes collected in all five main horizons of the platy and laminated limestones are for the most part well preserved. Complete specimens are common besides fish fragments, however the scales are usually missing or they are dispersed in the surrounding rock. The best preserved specimens were found in the Tomaj limestone at Križ and Dobravlje, where a typical mass mortality is evidenced. A perfect preservation was feasible due to very quick burial of organisms into the finest carbonate mud,

lack of oxygen in the lower layers of the water column and absence of circulation on the bottom of the sedimentary environment. Therefore, chemical and bacterial decomposition was progressing rather slowly and normal benthic life on the sea bottom was not possible (gastropods, bivalves, worms, crustaceans etc.) that would contribute to the mechanic destruction of fish carcasses. The speed of fossilization processes was affected also by other favourable physical and chemical parameters (increased salinity, temperature etc.).

An accurate picture of fossilization conditions for all horizons of the Komen limestone is not yet possible, although complete and well preserved fish specimens are rarer than in the Tomaj limestone. The fact that the Komen limestone was in former times intensively exploited and the total quantity of all horizons of the Komen limestone of Kras is substantially greater than the one from the Tomaj limestone is the main reason for more frequent finds of fishes in the Komen limestone than in the Tomaj limestone. The Cenomanian-Turonian Komen pelagic limestone that in the area between Mali Dol and Kobjeglava represents only a minor part of the fish-bearing strata in the sense of sedimentary processes and occurrence of fossils has not been studied in detail.

Radovčić and co-workers (1983) in the study on the Upper Cretaceous fish-bearing platy limestones of central Dalmatia came to a similar conclusions to that reached in Kras. Undoubtedly, frequency and quality of the preserved fossil fishes in the platy and laminated carbon rich limestones of the Trieste-Komen plateau depends mainly upon hydrography, paleogeography and configuration of the sea bottom that can change over very short distances on a carbonate platform.

PALEONTOLOGICAL PART

Chondrichthyes

Rajiformes

"Rhinobatidae" indet.

(Pl. IX)

Material: BJ 1380

This specimen, described and illustrated

under the name *Rhinobatos* sp. in Jurkovšek & Kolar-Jurkovšek, 1995 (Pl. 1, fig. 1), is regarded here as an indeterminate "Rhinobatidae". The Cretaceous guitarfish-like batomorphs were generally placed in the genus *Rhinobatos*. However, the Cretaceous "Rhinobatidae" form a paraphyletic group, and none of the species belong to the extant genus *Rhinobatos* (Brito, personal communication). A more precise study of BJ 1380 is necessary to understand its phylogenetic affinities among the primitive rays.

Hybodontiformes
Ptychodontidae
Ptychodus sp.
(Pl. I, fig. 1)

Material: BJ 2178

This isolated tooth has a subrectangular crown bearing a series of distinctively marginal enameloid ridges. This pattern is typical of the ptychodontid teeth, and we refer BJ 2178 to *Ptychodus* sp. with caution.

Osteichthyes
Actinopterygii
Pycnodontiformes

Material: BJ 517, BJ 1491, BJ 2015

Three isolated dentitions may be referred to pycnodont fishes: BJ 517 is made up of three rows of ellipsoidal to sub-rectangular teeth, BJ 1491 consists of a central row of ellipsoidal teeth bordered on each side by two rows of sub-circular teeth (partially visible on one side), while BJ 2015 is formed by a row of four ellipsoidal, decreasing in size, teeth. BJ 517 and BJ 2015 are "splenial" or prearticular dentitions according to the nomenclature proposed by Nursall (1999), and BJ 1491 is a vomerine dentition.

Several species of pycnodontiforms have been mentioned in the Komen plateau by Heckel (1856), Gorjanović-Kramberger (1895) and D'Erasmio (1952). These species were included in the genus *Coelodus*, and have been described mainly on complete or subcomplete specimens.

Pycnodontidae
Coelodus saturnus Heckel
(Pl. I, fig. 2)

Material: BJ 517

This dentition is similar to the dentition visible on a complete specimen of *Coelodus saturnus* illustrated by Heckel (1856, Pl. III, figs. 1-2), and to an isolated lower jaw dentition of the same species illustrated by D'Erasmio (1946).

Remark: Prof. Dr. Stanko Buser collected the specimen in the vicinity of Kobjeglava. Precise stratigraphic level of the Komen limestone is not certain.

Pycnodontiformes indet.

Material: BJ 1491, BJ 2015

These two specimens are much too incomplete to be determined at the specific and generic levels. They are regarded here as indeterminate pycnodontiforms.

Teleostei
Aspidorhynchiformes
Aspidorhynchidae
Belonostomus lesinaensis Bassani
(Pl. I, fig. 3)

Material: BJ 2194

The specimen is poorly preserved: bone material of the anterior part of the head and of elements of the caudal region are preserved, but no sutures are visible. The outline of the trunk is visible as a light trace in the matrix. The general morphology, and in particular the presence of a thin rostrum, is typical of aspidorhynchids. Because the premaxilla is only slightly more elongated than the predentary, this specimen may be referred to the genus *Belonostomus*. A single species is mentioned from the Komen plateau (D'Erasmio, 1946), *B. lesinaensis*, to which our specimen is referred with caution.

Ichthyodectiformes
Ichthyodectidae
Chirocentrites
Chirocentrites coronini Heckel
(Pl. II, fig. 1)

Material: BJ 2000

This large specimen is an almost complete elongated fish showing parts of the body with bone preserved and other parts preserved as negatives. It displays a typical

ichthyodectid outline, the head length included ca 6 times in standard length and the maximum depth is about 17% the standard length. The head profile is blunt, the first ray of the pectoral fin is broad and heavy, and there are about 33 abdominal and 28 caudal vertebrae. All these characters are diagnostic of *Chirocentrites* (Bardack, 1965). The anal fin is long and falcate, opposed by a short remote dorsal fin. According to Stewart (1999), this character is present in primitive ichthyodectiforms (*Occithrisops*, *Allothrisops*, *Thrissops* and *Cladocyclus*), but not in the more derived forms where the anal fin is short (Stewart unfortunately did not include *Chirocentrites* in his phylogenetic analysis). Two species of *Chirocentrites* have been mentioned in the Upper Cretaceous of the Trieste-Komen plateau until now (but see the discussion of *C.?* *microdon* below): *C. coronini* and *C. vexillifer* (according to the description of *C. gracilis* by Heckel (1850), this species is regarded here as a probable synonyme of *C.?* *microdon*). *C. vexillifer* was first assigned to the genus *Chirocentrites* by Heckel (1850, 1856) and Kner (1867), then regarded as a *Thrissops* by subsequent authors, and finally readmitted in the genus *Chirocentrites* by Taverne (1986). BJ 2000 may be referred to *C. coronini* because the lower jaw shows traces of elongated and pointed teeth, whereas the jaws are edentulous in *C. vexillifer*, and the dorsal fin starts well posterior to the beginning of the anal fin, whereas in *C. vexillifer* it starts barely posterior to the beginning of the anal fin (Taverne, 1986).

Chirocentrites?

Chirocentrites? microdon Heckel
(Pl. VIII, fig. 1)

Material: BJ 1521

This complete specimen (illustrated in Jurkovšek & Kolar-Jurkovšek, 1995, Pl. 2, fig. 2 and Jurkovšek et al., 1996, Pl. 11, fig. 2) may be referred with doubt to *C.?* *microdon* because of the position and the shape of the dorsal and anal fins, of the number of vertebrae (ca 58 without the ural ones), of the convex oral margin of the maxilla (Heckel, 1850,

D'Erasmio, 1946). This species was first mentioned in the Upper Cretaceous of the Trieste-Komen plateau under the generic name *Chirocentrites* (Heckel, 1850), then under the name *Thrissops* by Heckel (1856) and subsequent authors. However, according to the works of Taverne on *Thrissops* (1977) and on *Chirocentrites vexillifer* (1986), we can suspect that *C. microdon* is closer to the genus *Chirocentrites* than to the genus *Thrissops*: the vertical limb of the preopercular is poorly developed, while the horizontal limb is well developed, the symphysis is relatively deep and the trunk is elongated and slender (according to observations made on BJ 1521, to the plates XVI and XVII of Heckel (1850), and to figure 15 in D'Erasmio, 1946).

Further works will be necessary to confirm or invalidate whether *C.?* *microdon* is actually a *Chirocentrites* or if it belongs to another genus. In any case, it is very unlikely that this species belongs to the Late Jurassic genus *Thrissops*.

Ichthyodectidae indet.

(Pl. II, fig. 2, 3)

Material: BJ 396, BJ 1659, BJ 1730, BJ 2198

BJ 2198 is a subcomplete specimen with elements of the squamation. The scales are large, ovoid, and deeper than long, the vertebrae are numerous and longer than high and a supraoccipital crest is present, all these characters being ichthyodectid features. A notch is present on the anterior margin of the hyomandibular, ventrally to the anterior extremity of the articular facet. As far as we know, this feature has never been described in an ichthyodectid.

BJ 396, BJ 1730, BJ 1659 are parts of skeletons, which are referred with caution to indeterminate ichthyodectids.

Euteleostei indet.

(Pl. III, Pl. IV, figs. 1, 2)

Material: BJ 1737, BJ 2179, BJ 2211

BJ 1737 is the best example of mass mortality in our sample: it shows 15 complete or subcomplete individuals on a single slab. These small fishes are not well preserved and show no salient character. They can be excluded from the Cretaceous clupavids be-

cause they show no modifications of elements associated with the first vertebrae (Gayet, 1981, Cavin, 1999), from the clupeomorphs because they have no scutes (Grande, 1985), from the otophysi because the hypural 2 is not fused to the compound ural centrum (Fink & Fink, 1996), and from the acanthomorphs because there is no spine in front of the fins.

On the available specimens, few characters are visible, but all fit with the osteology of primitive Cretaceous euteleosts, such as *Ginsburgia* ("*Humbertia*") *operta* described by Patterson from the Cenomanian of Lebanon (the genus was re-named by Gayet in 1988): the body proportions; the orbitosphenoid and an ossified sclerotic are present; the metapterygoid is not reduced; the quadrate condyle is below the centre of the orbit; the gape is small; the mandible has a long and high coronoid process; PU2 bears a short, leaf-like neural spine; PU1 and U1 are fused, and U2 is separate; there are about 6 autogenous hypurals and probably 3 epurals; large caudal scutes are present; etc.

The material under study from the Tomaj limestone does not allow us to provide a precise description. It is however likely that this form differs from the oldest (Cenomanian) *G. operta* from Lebanon. For instance, no teeth are visible on our specimens, contrary to *G. operta*, which has an unusual mandibular dentition.

Patterson (1970) discussed the relationships between *G. operta*, *Gaudryella gaudryi*, both from the Cenomanian of Lebanon, and *Leptolepis neocomensis* Bassani, 1879 from the Komen plateau described by D'Erasmus (1946). *L. neocomensis* from Komen is regarded by Patterson as an euteleost differing from *G. operta* and *G. gaudryi* by a different vertebral count and the body proportions. One specimen of "*Clupea*" (= *Gaudryella*) *gaudryi* was mentioned by Gorjanović-Kramberger (1895) in the Komen area. It was then regarded as a *L. neocomensis* by D'Erasmus (1946) and Calligaris (1992), and was not discussed by Patterson (1970). *L. chechchai*, from the Komen plateau, was described by D'Erasmus (1946), then by Calligaris (1992). It differs from our specimens because there is a

complete neural spine on PU2 (Patterson, 1970).

The monophyly of euteleostei is still weakly supported (Lecointre & Nelson, 1996, Johnson & Patterson, 1996), and the assigning of our specimens to indeterminate euteleost rests more on similarities shared with other primitive euteleosts than on observed well defined euteleost synapomorphies.

Neoteleostei
Aulopiformes
Enchodontoidae
Enchodontidae
Enchodus sp.

(Pl. V, fig. 1, Pl. VI, figs. 1-3)

Material: BJ 1408, BJ 1522, BJ 1552, BJ 1738, BJ 1739, BJ 1791, BJ 2180, BJ 2204

The most informative specimen is BJ 2180, an acid prepared individual showing the head and most of the trunk region (the caudal skeleton is missing). The length of the head is only just greater than the depth at the occiput (the measurements are estimated on our specimen because the bones are slightly shifted). The mandible is long and shallow, its maximum depth being one fifth of its total length. The anteriormost tooth is more than twice as high as the other teeth: it is laterally compressed and slightly sigmoidal in lateral view. The symphysis is constricted and its ventral surface bears three finger-like processes increasing in size posteriorly. Longitudinal ridges radiate from the anterior and postero-ventral edges of the mandible on the lateral face. The remainder of the oral margin bears at least 8 large teeth and laterally a row of about 40 minute teeth. Both premaxillae are visible; the right one is shifted and turned over the skull roof. The anterior face of the premaxilla bears tiny tubercles as in *E. venator* (Arambourg, 1954) and *E. marchesetti* (Goody, 1969). The oral margin bears a row of more than 40 minute teeth. No premaxillary fenestra (which usually housed the largest anterior mandibular tooth in enchodontids) seems to be present on our specimen. A fragment of a narrow and elongated bone bearing more than 20 minute teeth lies across the posterior part of the oral margin of the mandible and par-

allel to the ectopterygoid: its shape and position indicate that it is possibly a piece of maxilla. Maxillae are generally very slender and edentulous in enchodontids (the edentulous condition is unclear in *E. venator* according to A r a m b o u r g, 1954). The ectopterygoid bears at least five teeth slightly larger than the mandibular teeth. A piece of the palatine is visible showing the base of the single, enlarged, terminal tooth typical of enchodontoids.

Elements of the skull roof, of the suspensorium, of the opercular series, of the branchiostegal rays are visible but not very informative.

Three different *Enchodus* species have been reported from the Trieste-Komen plateau (D' E r a s m o, 1946): *E. dentex*, *E. lycodon*, cf. *E. major*. They are however unsufficiently described to be compared with BJ 2180.

Other more incomplete specimens may be referred to *Enchodus* sp. BJ 2204 is an anterior half of a lower jaw bearing the typical huge enchodontid fang at its anterior tip. The size of this piece indicates a quite large fish, ca. 40 centimeters in standard length if the body proportions of *E. marchesetti* are used (G o o d y, 1969).

BJ 1408 is the posterior half of a fish. The first anterior haemal spines articulating with the anal pterygophores show proximal enlarged blades. This feature is derived among teleosts and is observed, as far as we know, only in enchodontids such as *Parenchodus* from the Cenomanian of Israel (R a a b & C h a l i f a, 1987). It is here referred with caution to *Enchodus* sp.

BJ 1522, BJ 1552, BJ 1738, BJ 1739, BJ 1791, BJ 2209 are parts of skeletons showing either the typical dentition or the typical haemal spines of enchodontids: they are referred here to *Enchodus* sp.

Cimolichthyoidei
Dercetidae
Rhynchodercetis sp.
(Pl. VIII, fig. 2)

Material: BJ 1517, BJ 1575

These two specimens are referred to the genus *Rhynchodercetis*, because of their very elongated and thin rostrum, the shape of the skull roof (BJ 1517), and the particu-

lar vertebrae with a laterally well developed processus of the haemapophysis. D' E r a s m o described *Rhynchodercetis* (= "*Leptotrachelus*") *gortani* (1946), then *R. acutissimus* (1952) from the Trieste-Komen plateau. Until more detailed studies on these specimens can be carried out, we refer them to *Rhynchodercetis* sp. BJ 1517 is illustrated in J u r k o v š e k & K o l a r - J u r k o v š e k, 1995, Pl. 2, fig. 1 under the name *Aspidorhynchidae*.

Acanthomorpha
Beryciformes
Hoplopteryx stachei
(Gorjanović-Kramberger)
(Pl. VII, fig. 1)

Material: BJ 1566

This specimen shows ca. 13 abdominal vertebrae and 11 caudal ones (without the ural ones), about 11 spines in front of the dorsal fin and a wide spine in front of the anal fin. These characters agree with the description of *Hoplopteryx stachei*, an acanthomorph fish described from the Trieste-Komen plateau by Gorjanović-Kramberger (1895), then by D' E r a s m o (1946) and Calligaris (1992).

Acanthomorpha indet.
(Pl. VII, fig. 2)

Material: BJ 1535, BJ 1725

BJ 1535 is a poorly preserved specimen showing spines in front of the pectoral and dorsal fins at least, and with about 20 vertebrae. BJ 1725 is a small interesting specimen showing more than 15 spines in front of the anal fin and some spines in front of the dorsal fin (Pl. VII, fig. 3). Both specimens are unfortunately too poorly preserved to be determined: they are regarded here as indeterminate acanthomorphs.

Teleostei indet.

Material: BJ 1387, BJ 1587, BJ 1761, BJ 2192

The general morphology and the layout of the caudal skeleton of these small fishes indicate that they are teleosts. However their state of preservation do not allow us to make more precise determination. They are regarded here as indeterminate teleosts.

taxa levels	"Rhino- batidae" indet.	<i>Ptychodus</i> sp.	<i>Coelodus</i> <i>saturnus</i>	<i>pycnodontiforms</i> indet.	<i>Belonostomus</i> <i>lesinaensis</i>	<i>Chirocentrites</i> <i>coronini</i>	<i>Chirocentrites</i> ? <i>microdon</i>	<i>ichthyodectids</i> indet.	<i>euteleostei</i> indet.	<i>Enchodus</i> sp.	<i>Rynchodercetis</i> sp.	<i>Hoplopteryx</i> <i>stachei</i>	<i>Acanthopterygii</i> indet.	<i>teleostei</i> indet.	indeterminate
TA/K ₂ ⁴⁻⁵ -TOMAJ LIMESTONE U. Santonian - L. Campanian	1380		1491		1521	1316 1737 1659 2179 1730 2211 2198	1408,1522 1552,1738 1739,1791 2180,2209				1517 1566 1575	1535 1761 1725	1317,1386,1524,1553 1565,1655,1664,1729 1849,1866,1872,1969 2210		
KA/K ₂ ⁴ -KOMEN LIMESTONE Santonian													1387 1472		
KA/K ₂ ³ -KOMEN LIMESTONE Coniacian			517 ?												
KPA/K ₂ ¹⁻² -KOMEN PELAGIC LIMESTONE Cenomanian - Turonian		2178						2204					2212		
KA/K ₂ ³ -KOMEN LIMESTONE Cenomanian				2015 2194 2000			396						1587 395 2192		

Fig. 3. List of fossil fishes stored in the Paleontological collection Jurkovšek with their catalogue number and stratigraphic location

Fig. 3. Seznam fosilnih rib iz Paleontološke zbirke Jurkovšek z njihovo kataloško številko in stratigrafskim položajem

DISCUSSION

Precise locations of all old fish finds are unknown, but we believe they were mainly collected in the Komen limestone of the north-western area of the Trieste-Komen plateau (Fig. 1). Most outcrops of Komen limestone in this area are Cenomanian or Cenomanian-Turonian in age. The specimens (about 74%) discussed in this paper were sampled in the Santonian-Campanian limestone, in the southward situated area between Kazlje, Dobravlje and Tomaj, and thus they represent a new fish assemblage if compared to the old collections.

About 40% of the specimens of the collection under study are not determinable. Few of the remaining ones (ca 10%) have been determined at the specific level and the others at the generic or familial levels (Figs. 2, 3). However we can discern a general pattern in the evolution of fossil assemblages between the Cenomanian Komen limestone and the Upper Santonian - Lower Campanian Tomaj limestone. (1) The enchodontids are very rare in the Komen limestones and became proportionally abundant in the Tomaj limestone. (2) The ichthyodectids are present through the whole section, but the species differ be-

tween the Cenomanian Komen limestone and the Tomaj limestone. Further studies of this lineage are necessary to observe whether the different ichthyodectid forms differ at the specific level or at a higher level. (3) The small indeterminate euteleosts appear in the fossil record in the Tomaj limestone. However, we should point out that small leptolepid-like fishes have been sampled in the Cenomanian Komen limestone (for instance BJ 2192), but their state of preservation is not good enough to determine whether they are true euteleosts or more basal teleosts. (4) According to our sample, the acanthomorphs appear in the fossil record in the Tomaj limestone. The first acanthomorphs are known in the Cenomanian, and it is likely that their absence in our sample is a sampling artefact.

Further studies of new finds and revisions of old collections will precise the changes observed in the fish assemblages of the Trieste-Komen limestone between the Cenomanian and the Upper Santonian-Lower Campanian.

CONCLUSION

Fossil fishes from the Trieste-Komen plateau have been known and studied for a long time, and the present review is a contribution to this knowledge. The study of new collection does not provide important anatomical or phylogenetic results, mainly because tiny details of skeletons are often poorly preserved. But this work is the first attempt to locate precisely the finds in the stratigraphic column of the Trieste-Komen plateau, and allows detecting the changes of the faunal composition in this area between the Cenomanian and Upper Santonian-Lower Campanian. It represents the first step in building a temporal framework in which the old and new finds of the Trieste-Komen plateau could be situated when their location is precise enough. The possibility to study the evolution of fish assemblages in a restricted geographical area is especially in-

formative because the paleoenvironments seem to have been relatively constant during a time span of 10 millions years of sediment deposition and due to high intensity of geological investigations of the area.

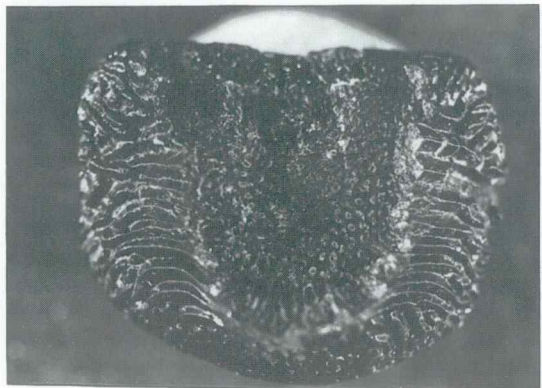
ACKNOWLEDGEMENTS

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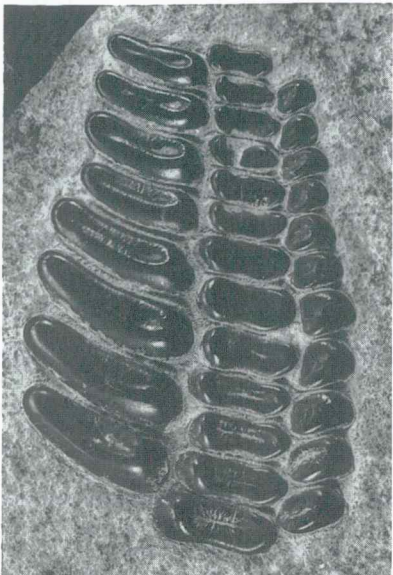
Plate I - Tabla I

- 1 *Ptychodus* sp., BJ 2178
Acid preparation / kislinška preparacija
Komen pelagic limestone, Cenomanian - Turonian
Komenski pelagični apnenec, cenomanij - turonij
Kobjeglava - Tomačevica. Scale bar / merilo: 10 mm
- 2 *Coelodus saturnus* Heckel, BJ 517
Komen limestone, Coniacian (?)
Komenski apnenec, coniacij (?)
Kobjeglava (?). Scale bar / merilo: 10 mm.
- 3 *Belonostomus lesinaensis* Bassani, BJ 2194.
Komen limestone, Cenomanian
Komenski apnenec, cenomanij
Volčji Grad. Scale bar / merilo: 10 mm

1



2



3



STRATIGRAFSKO ZAPOREDJE ZGORNJEKREDNIH RIBJIH ZDRUŽB KRASA (SLOVENIJA)

UVOD

O fosilnih vretenčarjih v ploščastih in laminiranih apnencih Tržaško-komenske planote je bilo napisanih že mnogo poljudnih člankov ter daljših in krajših znanstvenih razprav. Prvi zapisi segajo v prvo polovico devetnajstega stoletja (glej: Calligaris, 1994, Calligaris et al., 1994). Leta 1895 je Gorjanović-Kramberger v delu *Fosilne ribe Komena, Mrzleka, Hvara i M. Libanona* prvič podrobneje predstavil primerke iz Komna (in okolice), ki mu jih je v raziskavo odstopil Tržaški muzej. O posameznih najdbah fosilnih rib in plazilcev so pogosto poročali tudi nekateri drugi geologi druge polovice devetnajstega stoletja. Med njimi so bili Heckel (1850, 1856), Steindachner (1860), Kner (1863, 1867), Bassani (1879, 1880) in drugi. Študijo o muzejski zbirki fosilnih rib iz okolice Komna in Gorice, ki je danes v lasti Mestnega naravoslovnega muzeja v Trstu (70 primerkov), je objavil Calligaris (1992). Mnogo

primerkov iz te zbirke je bilo najdenih že v devetnajstem in prvi polovici dvajsetega stoletja.

Glede na to, da so na Tržaško-komenski planoti v devetnajstem stoletju in v začetku dvajsetega stoletja delovali številni manjši kamnolomi, v katerih so pridobivali apnenčeve plošče za kritino in tlakovanje, so bile tudi najdbe fosilnih rib razmeroma pogostne. Zaradi rib in skrilavega izgleda kamnine jih je Gorjanović-Kramberger (1895) imenoval ihtioferne skrilavce in uvedel to ime v znanstveno literaturo. Obenem je načel problematiko o starosti plasti z ribami, ki je ostala nerešena še dolga desetletja. Menil je, da "skrilavci" Komna in Mrzleka s svojo favno predstavljajo istodobne sedimente istega horizonta zgornje krede (? cenomanija), ki mu velja prišteti tudi druga kraška nahajališča temnih skrilavcev. Za istodobnost lokalitet se je odločil na osnovi ozke povezanosti teh plasti z rudistnimi apnenci ter zaradi njihove petrografske in favnistične podobnosti.

Tudi kasnejšim raziskovalcem ni bila povsem jasna natančna starost in stratigrafski položaj ploščastih in laminiranih apnencev Tržaško-komenske planote. D'Erasmo (1946), ki je raziskoval paleontološki del Hollerjeve privatne zbirke iz

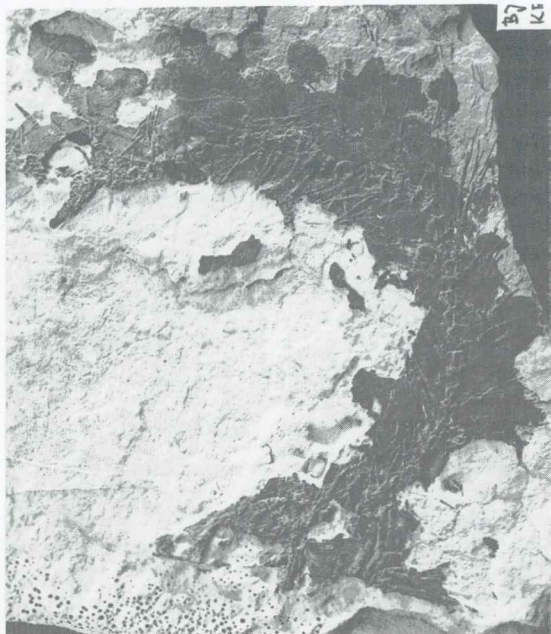
Plate II - Tabla II

- 1 *Chirocentrites coronini* Heckel, BJ 2000
Komen limestone, Cenomanian
Komenski apnenec, cenomanij
Gabrovica. Scale bar / merilo: 50 mm
- 2 Ichthyodectidae indet., BJ 2198
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Križ. Scale bar / merilo: 10 mm
- 3 Ichthyodectidae indet., BJ 396
Komen limestone, Cenomanian
Komenski apnenec, cenomanij
Tomačevica. Scale bar / merilo: 10 mm

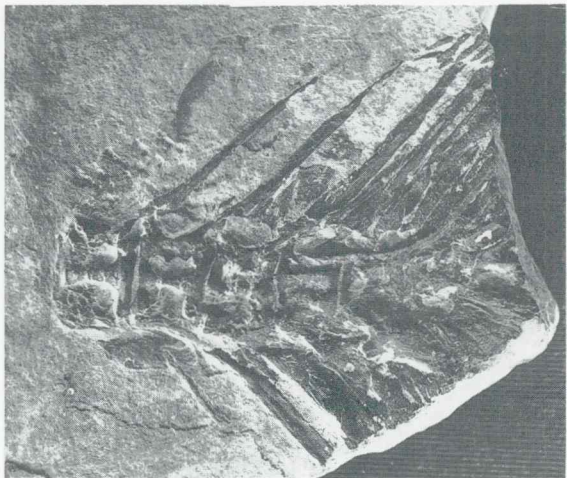
1



2



3



začetka dvajsetega stoletja (ta je kasneje prešla v last Geološkega muzeja Univerze v Bologni) je opisal fosilne ribe Kobjeglave, Komna, Križa, Malega Dola, Gabrovice, Jablanca, Rubij, Škrbine, Svetega, Tomačevice in Volčjega Gradu. Opisane lokalitete z ribami stratigrafsko obsegajo plasti od cenomanija do zgornjega santonija, morda celo do spodnjega campanija, kar pomeni več kot 10 milijonov let razlike v starosti med najstarejšimi in najmlajšimi najdbami.

Šele Pleničar (1960) je zapisal, da "komenski skrilarci niso stratigrafski horizont, ampak posebna facialna oblika senonskih, turonijskih in morda cenomanijskih in spodnjekrednih sedimentov". Ta ugotovitev je bila kasneje v osnovi potrjena tudi ob izdelavi Osnovne geološke karte 1: 100.000 list Gorica (Buser, 1968, 1973).

Raziskave za Formacijsko geološko karto 1 : 50.000 južnega dela Tržaško-komenske planote so pokazale (Jurkovšek et al., 1996), da je nivojev ploščastih in laminiranih apnencev z rožencem mnogo več kot so prvotno domnevali, predvsem pa, da so vezani na različne pogoje in območja nastanka. Vzporedno z geološkim kartiranjem so bile opravljene številne paleontološke raziskave makrofosilov iz teh plasti. Med njimi so bile pogoste tudi fosilne ribe (Jurkovšek & Kolar-Jurkovšek, 1995). Ob koncu geoloških raziskav za novo geološko karto 1 : 50.000 bo omogočena natančna stratigrafska revizija vseh muzejskih primerkov rib s Tržaško-komenske planote, če je v evidenčnih knjigah navedeno njihovo natančno najdišče.

V tej razpravi so opisane najnovejše, večinoma še neobjavljene fosilne ribe iz krednih plasti Krasa (sl. 1). Fosili so shranjeni v Paleontološki zbirki Jurkovšek, ki je v skladu z veljavno zakonodajo registrirana

pri Ministrstvu za kulturo Republike Slovenije in Prirodoslovnem muzeju Slovenije.

Predmet tega pregleda ni prispevati izčrpane opise vsega fosilnega materiala, temveč oceniti sestave ribjih združb v stratigrafskem zaporedju apnencev Tržaško-komenske planote. Posebno pozornost smo posvetili tistim skupinam, pri katerih so na razpoložljivih primerkih vidne zanimive osteološke značilnosti (na primer pri Enchodontoidei) in tistim, katerih determinacija ima poseben pomen za razumevanje zaporedja ribjih združb (na primer nedoločeni Euteleostei).

STRATIGRAFSKI DEL

V širšem geotektonskem smislu Kras pripada Zunanjim Dinaridom, v ožjem tektonskem smislu pa ga lahko opredelimo kot Tržaško-komensko planoto (sinklinorij) ali Komensko naravno grudo.

Za geološko zgradbo Krasa so značilni pretežno kredni platformski karbonati, ki skupno presegajo 2000 m debeline. Večji del osrednjega Krasa pripada krednim formacijam, ki se med seboj vertikalno in lateralno izmenjujejo v odvisnosti od paleogeografskih in paleoekoloških razmer ter različnih lokalnih in globalnih vplivov na sedimentacijsko okolje. Med slednjimi so najbolj izrazite globalne spremembe morske gladine in oceanski anoksični dogodki, ki so se na različnih delih Dinarske karbo-natne plošče različno odrazili (Gušić & Jelaska, 1990, Jurkovšek et al., 1996).

Pri geološkem kartiranju za novo geološko karto Tržaško-komenske planote smo posebno pozornost posvetili temnim ploščastim in laminiranim apnencem z rožencem, ki se pojavljajo v več nivojih znotraj plastovitih platformskih karbona-

Plate III - Tabla III

Euteleostei indet., BJ 1737. Mass mortality / masovno umiranje
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Križ. Scale bar / merilo: 10 mm.



tov, ki pogosto vsebujejo rudiste. Različno debeli vložki teh kamnin se pojavljajo v navidez podobni litološki obliki znotraj različnih formacij, vse od cenomanija do zgornjega santonija oziroma spodnjega campanija.

Na osnovi raziskav sedimentacijskega okolja in mehanizmov nastanka recentnih, z ogljikom bogatih morskih skrilavcev sta *Arthur* in *Sageman* (1994) zaključila, da lahko te plasti nastajajo v petih večjih recentnih morskih okoljih. Od teh bi lahko na Krasu nastanek zgornjekrednih bituminoznih apnenec povezali le s področji "upwellinga" in priobalnih medplimskih prostorov. Ob tem je potrebno upoštevati tudi različne pogoje njihovega nastanka od konfiguracije dna, različne globine vode, povezave z okolnimi morji, vertikalne oscilacije vodnega stolpca, do značaja sedimentacije itd. Skupna značilnost vseh nivojev bituminoznega apnenca z ribami na Krasu so tanke plasti in pogosta prisotnost laminiranih plasti, ki dajejo apnencu skrilav izgled.

Fosilne ribe smo vzorčevali v petih nivojih Komenskega in Tomajskega apnenca (sl. 2).

1. Komenski apnenec (cenomanij)

Najstarejša nahajališča rib so v cenomanijskem nivoju Komenskega apnenca pri

Gabrovici, Tomačevici, Rubijah in Volčjem Gradu. Gre za značilne plitvovodne morske sedimente znotraj medplimskega in lagunskega okolja z nizko energijo vode. Pole laminita in stromatolita so lahko lokalno natrgane, ponekod so prisotne tudi plasti nadplimskega konglomerata. Pojavljajo se tudi gomolji in tanjše pole temnosivega in črnega roženca, ki je mikro- do kriptokristalen in ima delno ohranjeno strukturo prvotne kamnine. Cenomanijsko starost teh plasti opredeljujejo plasti s hondrodontami in foraminifera *Broeckina* (*Pastrikella*) *balcanica* Cherchi, Radoičić & Schroeder.

2. Komenski pelagični apnenec (cenomanij - turonij)

Naslednji je cenomanijsko-turonjski horizont ploščatega apnenca, ki smo ga pri geološkem kartiranju Tržaško-komenske planote poimenovali Komenski pelagični apnenec. Debel je od tri do štiri metre in leži znotraj srednesivega mikritnega apnenca, ki poleg številnih kalcisfer (kalcisferski apnenec) in pitonel pogosto vsebuje fosilne ostanke kalcitiziranih radiolarijev in sakokomid. Pelagični mikritni apnenec s kalcisferami je rezultat evstatičnega dviga morske gladine na meji med cenomanijem in turonijem (Haq et al., 1987), ki je povzročil potopitev številnih platform in

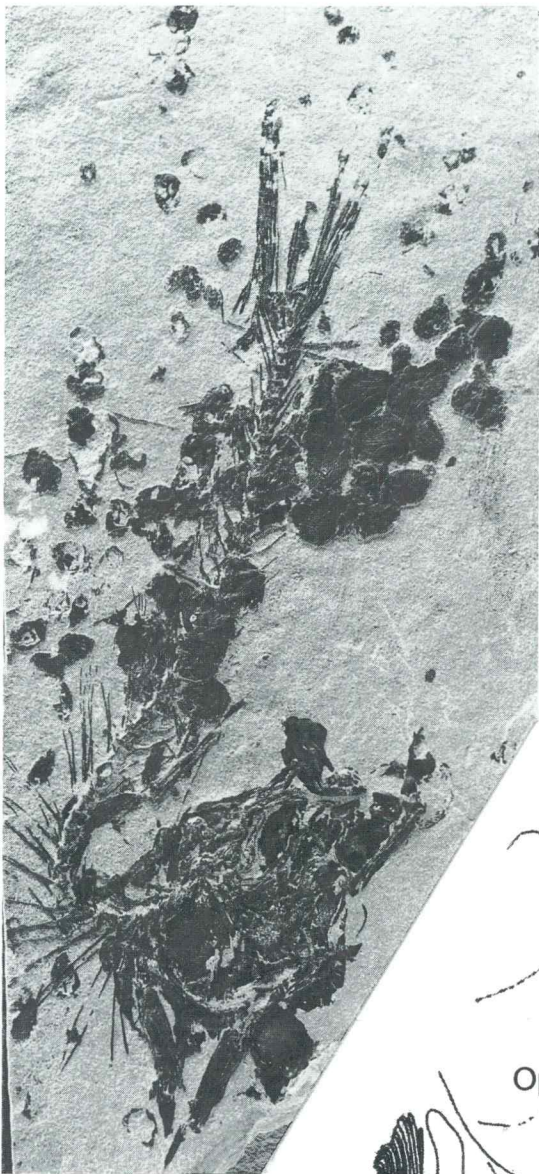
Plate IV - Tabla IV

- 1 Euteleostei indet., BJ 2211
 Photograph and drawing / fotografija in risba
 Acid preparation / kislinska preparacija
 Tomaj limestone, Upper Santonian - Lower Campanian
 Dobravlje, Scale bars / merila: 10 mm

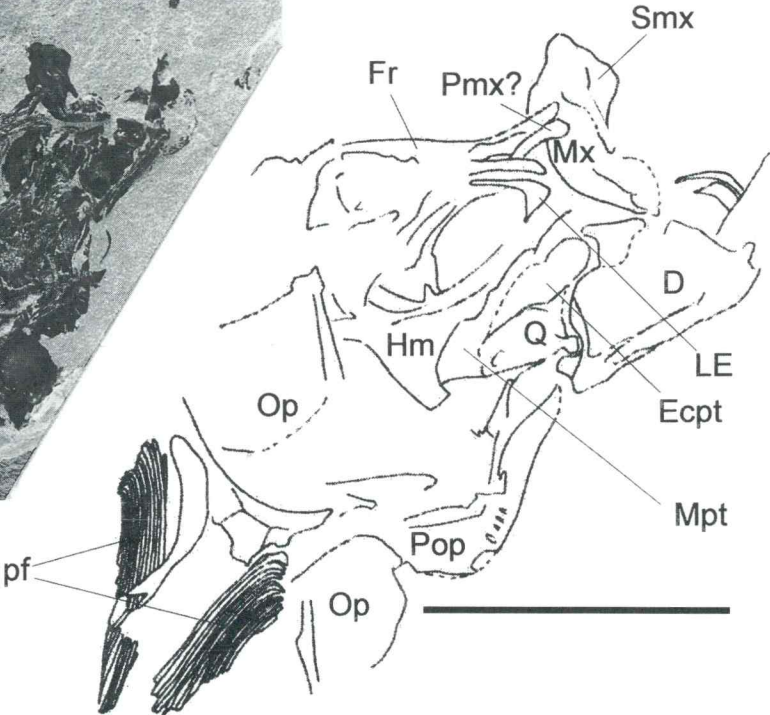
Abbreviations / Okrajšave: D - dentary, Ecpt - ectopterygoid, Fr - frontal, Hm - hyomandibular, LE - lateral ethmoid, Mpt - metapterygoid, Mx - maxilla, Op - opercule, pf - pectoral fins, Pmx - premaxilla, Pop - preopercule, Q - quadrate, Smx - supramaxilla

- 2 Euteleostei indet., BJ 2211
 Tomaj limestone, Upper Santonian - Lower Campanian
 Tomajski apnenec, zgornji santonij - spodnji campanij
 Križ. Scale bar / merilo: 10 mm

1



2



grebenov (Arthur & Schlanger, 1979, Jenkins, 1985, 1991, Weimer, 1988, Hine, 1997), med drugim tudi potopitev večjega dela Dinarske karbonatne platforme (Gušić et al., 1988, Gušić & Jelaska, 1990, 1993, Davey & Jenkins, 1999). Kalciferski apnenec se je odlagal v zelo mirnem okolju na potopljeni platformi. Z absolutnimi globlinami ne razpolagamo, vendar je bila globina vode tolikšna, da je potopila celotno bentoško bioto vezano na evfotično cono na karbonatni plošči.

Z ogljikom bogate plasti v okolici Komna so pogoto obravnavali med dokazi za drugi oceanski anoksični dogodek (OAE 2). Jenkins (1991) je na osnovi primerjave razmer na Dinarsko-jadranski karbonatni platformi in razmer v širšem mediteranskem prostoru sklepal, da je med cenomanijem in turonijem obstajala razmeroma debela plast anoksične vode, ki je v bazenu Umbria-Marche privedla do nastanka plasti Bonarelli (Montanari et al., 1995). OAE 2 je sestavljalo več anoksičnih dogodkov, ki so poleg glavnega (plast Bonarelli) povzročili nastanek še več tanjših, z ogljikom bogatih plasti.

Najnovejše raziskave na Krasu so pokazale, da se je glavni anoksični dogodek odrazil v sedimentaciji črnega ploščastega in laminiranega Komenskega pelagičnega apnenca, ki leži znotraj srednjesevega, plastovitega, mikritnega apnenca s kalcisferami. Lokalno so tudi v laminah Komenskega pelagičnega apnenca množično zastopane kalcisfere in pitonele. Fosilne ribe tega horizonta so bile vzorčevane na prostoru Tomačevica-Zajčnik

in Kobjeglava-Tomačevica. Od makrofosilov so poleg rib zastopani redki amoniti.

3. Komenski apnenec (coniacij)

Tretji horizont ploščastega in laminiranega apnenca z ribami pripada coniacijskemu Komenskem apnencu, ki se je odložil kmalu po globalni cenomanijsko-turonijski pelagični epizodi. V zgornjem turoniju je nagli padec evstatičnega nivoja morske gladine (Haq et al., 1987) povzročil sedimentacijo plitvodnih biomikritnih apnencev, pogosto z izsušitvenimi porami, in onkoidnih apnencev, ki so splošni značilni pojav na širšem prostoru in predstavljajo začetek sedimentacije Sežanske formacije. V spodnjem delu te formacije se pojavljajo tanjši vložki ploščastega, stromatolitnega in laminiranega apnenca s fosilnimi ribami.

4. Komenski apnenec (santonij)

Tudi četrti vzorčevani nivo Komenskega apnenca leži znotraj Sežanske formacije. V vasi Skopo se v štirimetrskem santonijemskem profilu Komenskega apnenca menjavajo plasti temnega biomikritnega apnenca, laminata, nadplimskega konglomerata in stromatolita. Pogosti so gomolji in pole roženca (Ogorelec et al., 1987). Od fosilov so zastopani rastlinski ostanki (golosemenke) in ribe.

5. Tomajski apnenec (zgornji santonij - spodnji campanij)

Peti horizont ploščastega in laminiranega apnenca z rožencem, imenovan tudi Tomajski apnenec, se pojavlja znotraj santonijsko-campanijske Lipiške formacije.

Plate V - Tabla V

Enchodus sp., BJ 2180

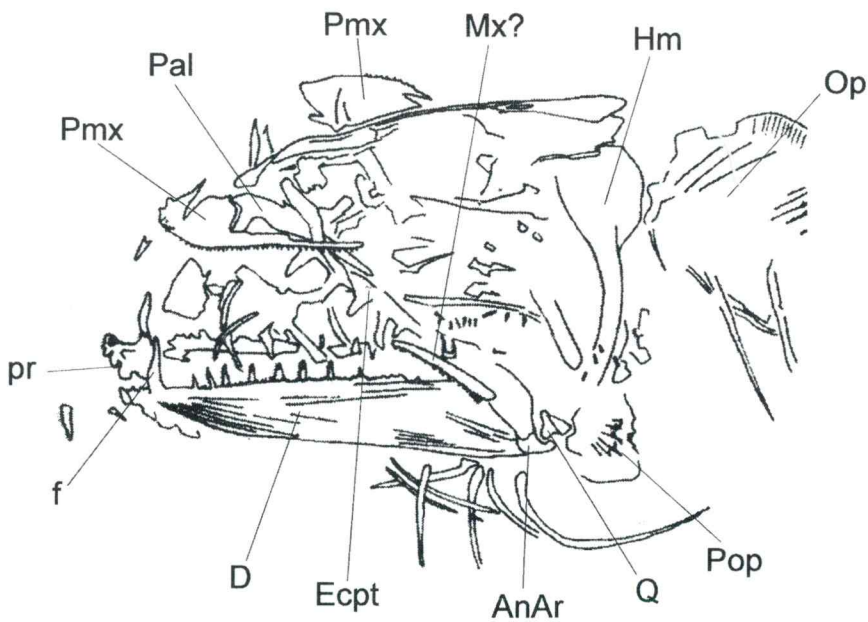
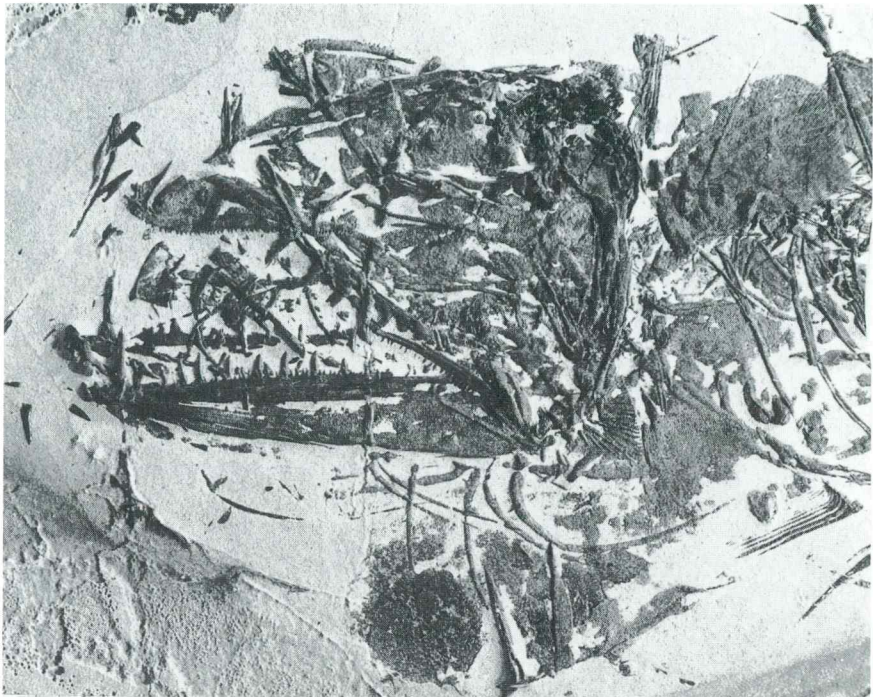
Photograph and drawing / fotografija in risba

Acid preparation / kislinska preparacija

Tomaj limestone, Upper Santonian - Lower Campanian

Dobrovlje, Scale bars / merila: 10 mm.

Abbreviations / Okrajšave: AnAr - angulo-articular, D - dentary, Ecpt - ectopterygoid, f - fang, Hm - hyomandibular, Mx - maxilla, Op - opercule, Pal - palatine, Pmx - premaxilla, Pop - preopercule, pr - finger-like process, Q - quadrate



Natančna interpretacija njegovega nastanka je še problematična, saj je povezava z evstatičnim dvigom morske gladine v tem delu Tetide še nedorečena. O nekoliko globljem sedimentacijskem okolju so na osnovi pojavljajočih alodapičnih apnencev sklepali že Ogorlec in sodelavci (1987), poleg tega pa v Tomajskem apnencu ni zaslediti znakov medplimskih razmer (Jurkovšek et al., 1996). Na dobro povezanost sedimentacijskega prostora z odprtim morjem kažejo pelagični mikro- in makrofosili, med katerimi prevladujejo amoniti z aptihi v bivalni kamrici, amonitni "roll marki", nepecljati krinoidi (Saccocomidae) ter drugi nektonski in planktonski organizmi, ki so živeli v vodnem stolpcu nad dnom z anoksičnimi razmerami (Jurkovšek & Kolar-Jurkovšek, 1995, Summesberger et al., 1996a, 1996b, 1999).

V nekaterih nivojih Tomajskega apnenca je bilo ugotovljeno množično umiranje organizmov (predvsem rib in sakokomid), ki ga povezujemo s premešanjem dobro stratificirane vode v laguni. Močan vpliv pelagiala v Tomajskem apnencu lahko na os-

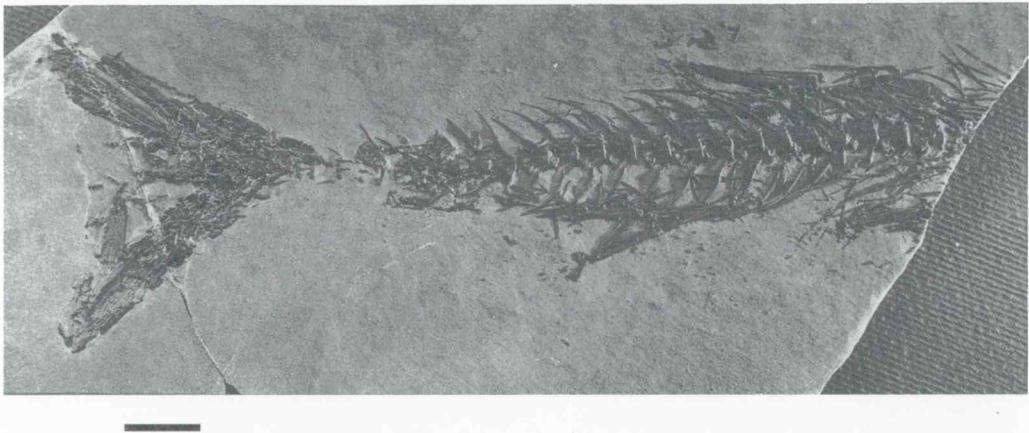
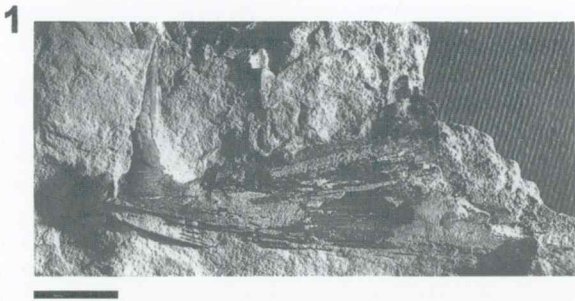
novi dosedanjih spoznanj povežemo tudi z rastjo morske gladine oziroma t.i. drugo pelagično epizodo na Dinarski karbonatni platformi v zgornjem santoniju in campaniju (Gušić & Jelaska, 1990, Kolar-Jurkovšek et al., 1996).

Od fosilov se poleg morskih organizmov v Tomajskem apnencu pojavljajo tudi številni rastlinski ostanki (Dobruskina et al., 1999), ki izvirajo iz kopna, ki je verjetno že v zgornjem santoniju pričelo nastajati južno od Tomajske lagune (Pleničar & Jurkovšek, 1997a, 1997b). Pri Dobravljah, Kazljah, Križu in Šepuljah so bile najdene številne fosilne ribe.

Zgornjesantonijska do spodnjecampanijska starost glavnega horizonta Tomajskega apnenca z ribami je na širšem prostoru določena z zgornjesantonijsko foraminifero *Murgella lata* (Luperto Sinni), ki je pogosta v plasteh pod Tomajskim apnencem ali lateralno v plasteh z rudisti, ki ustrezajo njegovemu nižjemu delu ter na osnovi campanijske vrste *Calveziconus lecalvezae* Caus & Cornella v krovnini Tomajskega apnenca (Šribar, 1995).

Plate VI - Tabla VI

- 1 *Enchodus* sp., BJ 2204
Anterior half of the lower jaw / sprednja polovica spodnje čeljusti
Acid preparation / kislinska preparacija
Komen pelagic limestone, Cenomanian - Turonian
Komenski pelagični apnenec, cenomanij - turonij
Tomačevica - Zajčnik. Scale bar / merilo: 10 mm
- 2 *Enchodus* sp., BJ 1408
Acid preparation / kislinska preparacija
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Dobravlje. Scale bar / merilo: 10 mm
- 3 *Enchodus* sp. and / in Saccocomidae, BJ 2209
Acid preparation / kislinska preparacija
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Dobravlje. Scale bar / merilo: 10 mm



FOSILIZACIJA

Fosilne ribe vseh petih glavnih horizontov ploščastega in laminiranega apnenca, ki smo jih vzorčevali, so večinoma dobro ohranjene. Poleg ribjih fragmentov so pogostni tudi celi primerki rib, vendar luske ponavadi manjkajo ali pa so razpršene v okoliški kamnini. Najbolje ohranjeni primerki so bili najdeni v Tomajskem apnencu pri Križu in Dobravljah, kjer beležimo tudi pojave masovnega umiranja. Odlični fosilizaciji so tam pripomogli razmeroma hitri pokop odmrlih organizmov v najfinejše karbonatno blato, pomanjkanje kisika v nižjih plasteh vodnega stolpca in odsotnost tokov pri dnu sedimentacijskega prostora. Zato je bila bistveno upočasnjena kemijska in bakterijska razgradnja ter onemogočeno normalno bentoško življenje na dnu (polži, črvi, školjke, raki itd.), ki bi prispevalo k mehanični destruktiji ribjih kadavrov. Na hitrost procesov fosilizacije so vplivali tudi drugi ugodni fizikalni in kemijski parametri (povišana saliniteta, temperatura itd.).

Za vse horizonte Komenskega apnenca trenutno še ni mogoče podati natančne slike fosilizacijskih razmer, čeprav so celi in lepo ohranjeni primerki rib redkejši kot v Tomajskem apnencu. Vzrok temu, da so bile najdbe fosilnih rib v Komenskem apnencu

v preteklosti pogostejše kot v Tomajskem je predvsem v tem, da so Komenski apnenec некоč intenzivneje izkopavali in da je skupna količina vseh horizontov Komenskega apnenca na Krasu bistveno večja od Tomajskega. Cenomanijsko-turonijski Komenski pelagični apnenec, ki na prostoru med Malim Dolom in Kobjeglavo predstavlja le manjši del plasti z ribami, v smislu sedimentacijskih procesov in pojavljanja fosilov še ni podrobno raziskan.

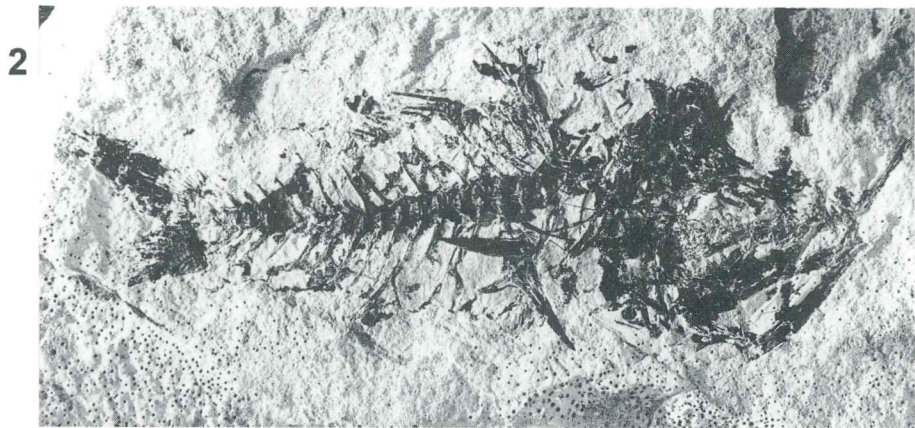
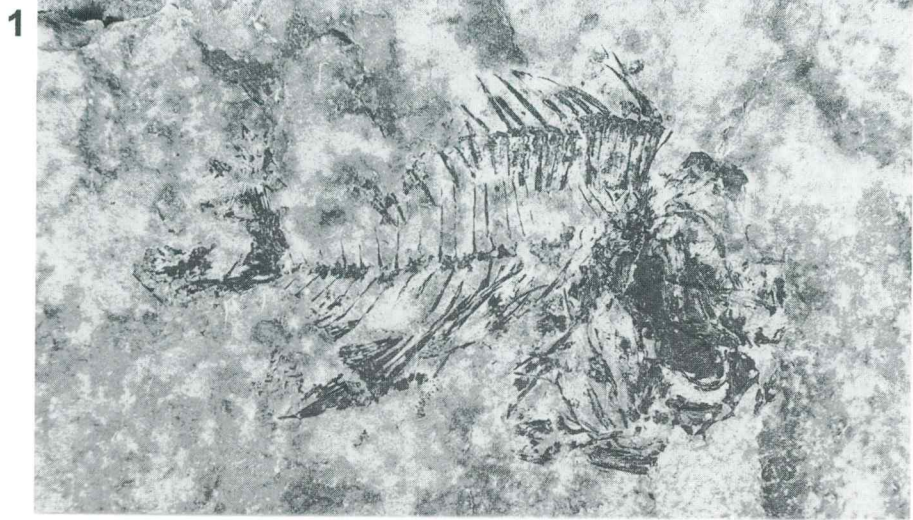
Radovčič in sodelavci (1983) so na primeru zgornjekrednih ploščastih apnencev z ribami v srednji Dalmaciji prišli do podobnih spoznanj kot jih preliminarno ugotavljamo na Krasu. Nedvomno zavisi pogostnost in kvaliteta ohranjenosti fosilnih rib v ploščastih in laminiranih, z ogljikom bogatih apnencih Tržaško-komenske planote predvsem od hidrografije, paleogeografije in od konfiguracije morskega dna, ki se je na karbonatni plošči spreminjalo na zelo kratkih razdaljah.

DISKUSIJA

Natančne lokalitete vseh starih najdb fosilnih rib niso znane, vendar menimo, da so bile v glavnem najdene v Komenskem apnencu severozahodnega dela Tržaško-

Plate VII - Tabla VII

- 1 *Hoplopteryx stachei* (Gorjanović-Kramberger), BJ 1566
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Kazlje. Scale bar / merilo: 10 mm
- 2 *Acanthomorpha* indet., BJ 1535
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Kazlje. Scale bar / merilo: 10 mm
- 3 *Acanthomorpha* indet., BJ 1725
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Dobravlje. Scale bar / merilo: 10 mm



komenske planote (sl. 1). Večina izdankov Komenskega apnenca na tem delu ozemlja je cenomanijske ali cenomanijsko-turonijske starosti. Primerki, ki jih obravnavamo v tem članku (približno 74%), so bili zbrani v južneje ležečem santonijsko-campanijskem Tomajskem apnencu med Kazljami, Dobravljami in Tomajem, zato v primerjavi s starimi zbirkami predstavljajo novo združbo rib.

Približno 40% primerkov v raziskani zbirki ni določljivih, nekaj (okoli 10%) je bilo vrstno določeno, vsi drugi pa so razpoznavni le na stopnji rodu ali družine (sl. 2, 3). Kljub temu lahko opazujemo splošno razliko v sestavi fosilnih združb med cenomanijskim Komenskim apnencem in zgornje-santonijsko-spodnjecampanijskim Tomajskim apnencem. (1) *Enchodontoidae* so zelo redki v Komenskem apnencu in so razmeroma pogostni v Tomajskem apnencu (2) *Ichthyodectidae* so prisotni v celotnem profilu Krasa, vendar se vrste v cenomanijskem Komenskem apnencu razlikujejo od vrst v Tomajskem apnencu. Z nadaljnjimi raziskavami te linije bo potrebno ugotoviti ali se različne oblike te skupine razlikujejo na nivoju vrste ali na višjem nivoju. (3) Majhni nedoločeni *Euteleostei* so bili najdeni v Tomajskem apnencu. Opozoriti je potrebno tudi na majhne leptolepidne oblike, ki so bile vzorčevane v cenomanijskem Komenskem apnencu (na primer BJ 2192). Žal njihova stopnja ohranjenosti ne omogoča opredelitve ali spadajo med prave euteleoste ali med bolj bazalne teleoste. (4) V naših vzorcih se *Acanthomorpha* pojavljajo

le v Tomajskem apnencu. Prvi predstavniki te skupine so znani iz cenomanija, zato obstoja možnost, da jih bomo našli tudi v Komenskem apnencu.

Nadaljnje študije novih najdb in revizija starih združb bodo bolj natančno pokazale na razlike, ki smo jih opazili že v tej fazi raziskav v ribjih združbah Tržaško-komenske planote med cenomanim in campanijem.

ZAKLJUČEK

Fosilne ribe s Tržaško-komenske planote so poznane že dolgo časa, zato ta pregled predstavlja le prispevek k njihovem poznavanju. Študij novih najdb ne omogoča pomembnih anatomskih in filogenetskih rezultatov predvsem zato, ker so podrobnosti skeletov pogosto slabše ohranjene. Predstavljeno delo je prvi poskus določitve natančnega položaja najdb v stratigrafskem stolpcu Tržaško-komenske planote, ki prispeva k poznavanju razlik v favnistični sestavi na tem območju med cenomanim in spodnjim campanijem. Predstavlja prvo stopnjo izdelave časovnega okvira, v katerega bodo lahko v prihodnosti uvrščene vse nove in stare najdbe fosilnih rib Tržaško-komenske planote, v kolikor bo njihov geografski položaj dovolj natančno določen. Možnost študija evolucije ribjih združb na omenjenem območju je posebno poučna zaradi razmeroma konstantnega paleoekoloja v razponu 10 milijonov let (med cenomanim in campanijem) in zaradi dobre geološke raziskanosti terena.

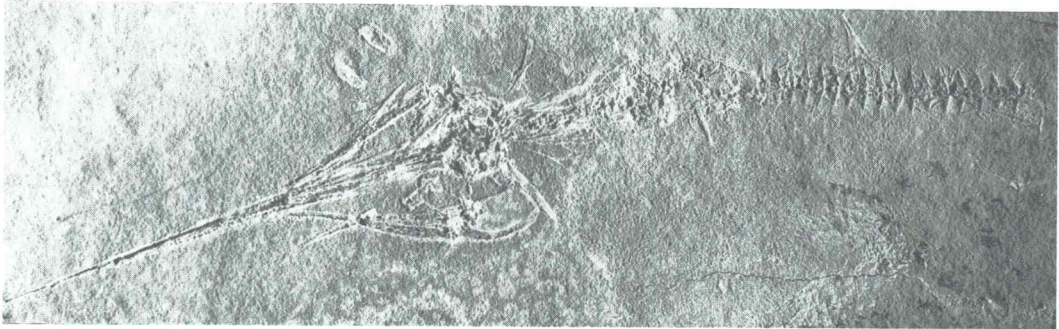
Plate VIII - Tabla VIII

- 1 *Chirocentrites? microdon* Heckel, BJ 1521
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Dobravlje. Scale bar / merilo: 10 mm
- 2 *Rynchodercetis* sp., BJ 1517
Tomaj limestone, Upper Santonian - Lower Campanian
Tomajski apnenec, zgornji santonij - spodnji campanij
Dobravlje. Scale bar / merilo: 10 mm

1



2



REFERENCES

- Arambourg, C. 1954: Les poissons crétacés du Jebel Tsfat (Maroc). - Notes et Mémoires, 118, 1-188, Rabat.
- Arthur, M.A. & Sageman, B.B. 1994: Marine Black Shales: Depositional Mechanisms and Environments of Ancient Deposits. - Ann. Rev. Earth Planet. Sci., 22, 499-551, Palo Alto.
- Arthur, M.A. & Schlanger, S.O. 1979: Cretaceous "Oceanic Anoxic Events" as Causal Factors in Development of Reef-Reservoired Giant Oil Fields. - Am. Assoc. Petrol. Geol. Bull., 63/6, 870-885, Tulsa.
- Bardack, D. 1965: Anatomy and evolution of Chirocentrid Fishes. - The University of Kansas Paleontological Contributions, 10, 1-88, Kansas.
- Bassani, F. 1879: Über einige fossile Fische von Comen. - Verh. k.k. geol. R.-A., 9, 204-205, Wien.
- Bassani, F. 1880: Contribuzione alla fauna ittologica del Carso presso Comen in Istria. - Atti. Acad. Sci. ven.-trent.-istr., 7/1, 1-15, Padova.
- Buser, S. 1968: Osnovna geološka karta SFRJ, list Gorica, 1:100.000. - Zvezni geološki zavod, Beograd.
- Buser, S. 1973: Tolmač lista Gorica. Osnovna geološka karta SFRJ 1:100.000. - Zvezni geološki zavod, 50 pp., Beograd.
- Calligaris, R. 1992: I pesci fossili dei calcari ittiolitici di Comeno e di facies a questa correlabili conservati nelle collezioni del Museo civico di Storia Naturale di Trieste. - Atti Mus. civ. Stor. Nat. Trieste, 44, 57-111, Trieste.
- Calligaris, R. 1994: 95 milioni di anni fa. Il periodo cretacico attraverso i fossili di Comeno ed altri reperti del Carso. - Museo civico di Storia Naturale di Trieste, 24 pp., Trieste.
- Calligaris, R., Krivic, K. & Pleničar, M. 1994: Fosili Tržaško-Komenskega Krasa. Ostanke živih bitij izpred 95 milijonov let. - Prirodoslovni muzej Slovenije, 40 pp., Ljubljana.
- Cavin, L. 1999: A new Clupavidae (Teleostei, Ostariophysi) from the Cenomanian of Daoura (Morocco). - C. R. Acad. Sci., Sci. Terre et Planètes, 329, 689-695, Paris.
- Davey, S.D. & Jenkyns, H.C. 1999: Carbon-isotope stratigraphy of shallow-water limestones and implications for the timing of Late Cretaceous sea-level rise and anoxic events (Cenomanian-Turonian of the peri-Adriatic carbonate platform, Croatia). - Eclogae geol. Helv., 92, 163-170, Basel.
- D'Erasmio, G. 1946: L'ittiofauna Cretacea dei dintorni di Comeno nel Carso triestino. - Atti R. Accad. Sc. fis. mat., 3a 2/8, 1-136, Napoli.
- D'Erasmio, G. 1952: Nuovi ittioliti cretacei del Carso Triestino. - Estratto dagli Atti del Museo Civico di Storia Naturale Trieste, 18/4, 81-122, Rocca San Casciano.
- Dobruskina I.A., Jurkovšek, B. & Kolar-Jurkovšek, T. 1999: Upper Cretaceous flora of Slovenia. - Annales, 17, 243-268, Koper.
- Fink, S.V. & Fink, W.L. 1996: Chapter 11. Interrelationships of Ostariophysan Fishes (Teleostei). In: M.L.J. Stiassny, L.R. Parenti & G.D. Johnson (eds.): Interrelationships of Fishes. - Academic Press, 209-249, San Diego.
- Gayet, M. 1981: Contribution à l'étude anatomique et systématique de l'ichthyofaune cenomanienne du Portugal. Deuxième partie: Les Ostariophysaires. - Comun. Serv. Geol. Portugal, 67/2, 173-190, Lisbon.
- Gayet, M. 1988: *Gharbouria libanica* nov. gen., nov. sp., "Salmonifforme" nouveau en provenance d'Ain-el-Gharbour, nouveau gisement cenomanien du Liban. - Bull. Mus. nat., 4e ser., sec. 3, 10/3, 199-225, Paris.
- Goody, P.C. 1969: The Relationships of certain Upper Cretaceous Teleosts with special Reference to the Myctophoids. - Bulletin of the British Museum (Natural History) Geology, Supplement 7, 1-255, London.
- Gorjanović-Kramberger, C. 1895: Fosilne ribe Komena, Mrzleka, Hvara i M. Libanona uz dodatke o oligocenskim ribama Tifera, Zagora i Trifalja. - Djela jugosl. akad. znan. umjet., 16, 1-67, Zagreb.
- Grande, L. 1985: Recent and Fossil Clupeomorph Fishes with material for revision of the subgroups of clupeoids. - Bulletin of the American Museum of Natural History, 181/2, 231-272, New York.
- Gušić, I. & Jelaska, V. 1990: Stratigrafija gornjokrednih naslaga otoka Brača u okviru geodinamske evolucije Jadranske karbonatne platforme. - Djela jugosl. akad. znan. umjet., Razr. prir. znan., 69, 1-160, Zagreb.

Plate IX - Tabla IX

"Rhinobatidae" indet., BJ 1380

Tomaj limestone, Upper Santonian - Lower Campanian

Tomajski apnenec, zgornji santonij - spodnji campanij

Dobravljje. Scale bar / merilo: 50 mm

All the photographs were taken by B. Jurkovšek

Vse fotografije je posnel B. Jurkovšek



Gušić, I. & Jelaska, V. 1993: Upper Cenomanian-Lower Turonian sea-level rise and its consequences on the Adriatic-Dinaric carbonate platform. - *Geol. Rund.*, 82/4, 676 - 686, Stuttgart.

Gušić, I., Jelaska, V. & Velić, I. 1988: Foraminiferal Assemblages, Facies, and Environments in the Upper Cretaceous of the Island of Brač, Yugoslavia. - *Rev. Paléobiol.*, Vol. Spéc. 2, Benthos '86, 447-456, Geneva.

Haq, B.U., Hardenbol, J. & Vail, P.R. 1987: Chronology of Fluctuating Sea Levels since the Triassic. - *Science*, 23, 1156-1167, Washington D. C.

Heckel, J.J. 1850: Beiträge zur Kenntniss der fossilen Fische Österreichs. Abhandlung I. - *Denkschr. k. Akad. Wiss., Math.-naturw. Cl. I.*, 201-242, Wien.

Heckel, J.J. 1856: Beiträge zur Kenntniss der fossilen Fische Österreichs. Abhandlung II. - *Denkschr. k. Akad. Wiss., Math.-naturw. Cl., Eilfter Band*, 187-274, Wien.

Hine, A.C. 1997: Chapter 11. Structural, Stratigraphic, Paleogeographic Development of the Margins of the Florida Platform. In: A.F. Randazzo & D.S. Jones (eds.): *Geology of Florida*. - University of Florida Press, Chapter 11, 35 pp., Gainesville.

Jenkyns, H.C. 1985: The Early Toarcian and Cenomanian-Turonian anoxic events in Europe: comparisons and contrasts. - *Geol. Rund.*, 74/3, 505 - 518, Stuttgart.

Jenkyns, H.C. 1991: Impact of Cretaceous Sea Level Rise and Anoxic Events in Mesozoic Carbonate Platform of Yugoslavia. - *Am. Assoc. Petrol. Geol. Bull.*, 75/6, 1007 - 1017, Tulsa.

Johnson, G.D. & Patterson, C. 1996: Chapter 12. Relationships of Lower Euteleostean Fishes. In: M.L.J. Stiassny, L.R. Parenti & G.D. Johnson (eds.): *Interrelationships of Fishes*. - Academic Press, 251-332, San Diego.

Jurkovšek, B. & Kolar-Jurkovšek, T. 1995: Zgornjekredni skat *Rhinobatos* iz Lipiške formacije pri Dobravljah (Tržaško-komenska planota, Slovenija). - *Annales*, 7, 161-170, Koper.

Jurkovšek, B., Toman, M., Ogorelec, B., Šribar, L., Drobne, K., Poljak, M. & Šribar, Lj. 1996: Formacijska geološka karta južnega dela Tržaško-komenske planote 1:50.000. Kredne in paleogenske karbonatne kamnine. - *Inštitut za geologijo, geotehniko in geofiziko*, 143 pp., Ljubljana.

Kolar-Jurkovšek, T., Jurkovšek, B. & Summesberger, H. 1996: Reflection of the two pelagic episodes in the macrofossil associations of the Komen and Tomaj limestones of the Trieste-Komen Plateau, Slovenia. In: K. Drobne, et al. (eds.): *The role of impact processes in the geological and biological evolution of planet Earth*. - International workshop, September 27 - October 2, 1996, Postojna/Slovenija, 41-43, Ljubljana.

Kner, R. 1863: Über einige fossilen Fische aus den Kreide- und Tertiärschichten von Comen und Podused. - *Sitzungsber. math.-naturw. Cl. k. Akad. Wiss.*, 48/1, 126-148, Wien.

Kner, R. 1867: Neuer Beitrag zur Kenntniss der fossilen Fische von Comen bei Görz. - *Sitzungsber. math.-naturw. Cl. k. Akad. Wiss.*, 56, Wien.

Lecointre, G. & Nelson, G. 1996: Chapter 10. Clupeomorpha, Sister-Group of Ostariophys. In: M.L.J. Stiassny, L.R. Parenti, & G.D. Johnson (eds.): *Interrelationships of Fishes*. - Academic Press, 193-207, San Diego.

Montanari, A., Coccioni, R. & Beaudoin, B. 1995: Stop 1. The Cenomanian/Turonian (C/T) boundary in the Furlo Upper Quarry. In: A. Montanari & R. Coccioni (eds.): *4th International Workshop of the ESF Scientific Network on "Impact Cratering and Evolution of Planet Earth"*. - Ancona, May 12-17, 1995, The Role of Impacts on the Evolution of the Atmosphere and Biosphere with Regard to Short- and Long Term Changes, Abstracts and Field Trips volume, 170-172, Ancona.

Nursall, J. R. 1999. The pycnodontiform bauplan: The morphology of a successful taxon. In: G. Arratia & H.-P. Schultze (eds.): *Mesozoic Fishes 2. Systematics and Fossil Record*. - Dr. Friedrich Pfeil, 189-214, München.

Ogorelec, B., Orehek, S., Buser, S. & Pleničar, M. 1987: Komen Beds - Skopo at Dutovlje (Upper Cretaceous). - "Evolution of the karstic carbonate platform", *Excursion Guidebook*, 61-66, Trieste.

Patterson, C. 1970: Two Upper Salmoniform fishes from the Lebanon. - *Bull. of the Brit. Mus. (Nat. Hist.)*, *Geology*, 19/5, 207-296, London.

Pleničar, M. 1960: Stratigrafski razvoj krednih plasti na južnem Primorskem in Notranjskem. *Geologija*, 6, 22-145, Ljubljana.

Pleničar, M. & Jurkovšek, B. 1997a: Eksogire s Tržaško-komenske planote. - *Geol. zbornik*, 13, 87-99, Ljubljana.

Pleničar, M. & Jurkovšek, B. 1997b: Rudisti iz Lipiške formacije v kamnolomu Lipica 1. - *Annales*, 11, 115-140, Koper.

Raab, M. & Chalifa, Y. 1987: A new Enchodontid fish genus from the Upper Cenomanian of Jerusalem, Israel. - *Palaeontology*, 30/4, 717-731, London.

Radović, J., Tišljarić, J. & Jelaska, V. 1983: Upper Cretaceous Fish-bearing Platy Limestones in Central Dalmatia. In: Lj. Babić & V. Jelaska (eds.): *Contributions to Sedimentology of Some Carbonate and Clastic Units of the Coastal Dinarides*. - Excursion Guidebook, 4th IAS Regional Meeting, Split 1983, 79-85, Zagreb.

Steindachner, F. 1860: Beiträge zur Kenntniss der fossilen Fische Österreichs. II. Über einen neuen Vomer-ähnlichen Fisch von Comen am Karst. - *Sitzungsber. math.-naturw. Cl. k. Akad. Wiss.*, 38 (1859), 763-788, Wien.

Stewart, J. D. 1999. A new genus of Saurodontidae (Teleostei: Ichthyodectiformes) from Upper Cretaceous rocks of the Western Interior of North America. In: G. Arratia & H.-P. Schultze: *Mesozoic Fishes 2. Systematics and Fossil Record*. - Dr. Friedrich Pfeil, 335-360, München.

Summesberger, H., Jurkovšek, B. & Kolar-Jurkovšek, T. 1996a: Aptychi associated with ammonites from the Lipica-Formation (Upper Cretaceous, Slovenia). - *Ann. Naturhist. Mus. Wien*, 97 A, 1-19, Wien.

Summesberger, H., Jurkovšek, B. & Kolar-Jurkovšek, T. 1996b: Association of aptychi and ammonites in Upper Cretaceous carbonates of Slovenia. - IV. International Symposium Cephalopods present and past, Abstract Volume, 161-162, Granada.

Summesberger, H., Jurkovšek, B. & Kolar-Jurkovšek, T. 1999: Rollmarks of soft parts and a possible crop content of Late Cretaceous ammonites from the Slovenian Karst. In: F. Oloriz & F.J. Rodriguez-Tovar (eds.): *Advancing Research on Living and Fossil*

Cephalopods. - Kluwer Academic / Plenum Publishers, 335-344, New York.

Šribar, L. 1995: Evolucija gornjokredne Jadransko-dinarske karbonatne platforme u jugozapadnoj Sloveniji. - Magistarski rad, Sveučilište u Zagrebu, 89 pp., Zagreb.

Taverne, L. 1977: Ostéologie et position systématique du genre *Thrissops* AGASSIZ, 1833 (sensu stricto) (Jurassique supérieur de l'Europe occidentale) au sein des Téléostéens primitifs. - *Geobios*, 10/1, 5-33, Lyon.

Taverne, L. 1986: Ostéologie et Affinités systématiques de *Chirocentrites vexillifer* du Crétacé supérieur de la Mésogée Eurafrique. Considération sur la phylogénie des Ichtyodectiformes, Poissons Téléostéens du Jurassique et du Crétacé." *Annls. Soc. r. zool. Belg.*, 116/1, 33-54, Bruxelles.

Weimer, R.J. 1988: Record of Relative Sea-Level Changes, Cretaceous of Western Interior, USA. In: C.K. Wilgus et al. (eds.): *Sea Level Changes. An Integrated Approach*. - SEPM, Spec. Publ. No. 42, 285 - 288, Tulsa.