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HARPACTOCARCINUS FROM THE EOCENE OF ISTRIA, CROATIA, AND THE PALEOECOLOGY OF THE ZANTHOPSIDAE VIA, 1959 (CRUSTACEA: DECAPODA: BRACHYURA)

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ABSTRACT—*Harpactocarcinus punctulatus istriensis* Bachmayer and Nosan, 1959 is elevated to species level. Analysis of the larger foraminiferans associated with specimens of *H. istriensis* suggests a habitat preference for off-shore, clear, shelf environments below fair-weather wave base and an age of early to middle Lutetian (Eocene). A review of the paleoenvironmental indicators for nearly all species within the genera referred to the Zanthopsidae Via, 1959 suggests that all exhibit similar habitat preferences. Description of the paleoenvironmental preference for an entire extinct decapod family has not before been possible.

INTRODUCTION

FOSSIL DECAPOD crustaceans have been reported from various localities in Istria (Croatia and Slovenia) on several occasions; however, these reports have been limited to nineteenth-century and early twentieth-century descriptions (Bittner, 1883, 1884, 1893; Stache, 1889; Toniolo, 1909; Vogl, 1912), anecdotal reports, and short notes (Salopek, 1954; Bachmayer and Nosan, 1959; Tarlao, 2000; Mikuž, 2002) (Table 1). Toniolo (1909) described numerous localities in Croatia from which decapods were collected, giving them Italian names that are no longer used (Table 2). The region would be expected to contain a robust decapod fauna, due to the presence of a well-developed carbonate ramp in the area during the middle Eocene (Ćosović et al., 2004) and the robust Eocene decapod record in nearby Hungary (Müller and Collins, 1991) and Spain (Via, 1959, 1969). However, the decapod record in Istria is surprisingly sparse (Table 1). All of the fossil decapods previously reported from localities in Istria are brachyurans, and the overwhelming majority of the occurrences are of species of *Harpactocarcinus* A. Milne Edwards, 1862 and *Harpactoxanthopsis* Via, 1959, both members of the extinct family Zanthopsidae Via, 1959. Specimens of *Lophoranina* sp. are also common (Bittner, 1893). *Harpactocarcinus* sp. and *Harpactoxanthopsis* sp. are so common that the layers in which they are found are known in the literature as the ''marls with crabs.'' The flysch deposits overlying the ''marls with crabs'' contain trace fossils referrable to *Ophiomorpha* Lundgren, 1891 and *Thalassinoides* Ehrenberg, 1944 (Tunis and Uchman, 1996), but no decapod fossils have yet been reported from the flysch sediments. Limestones of the underlying carbonate ramp sediments are primarily packstones containing numerous foraminiferans but they do not contain decapod fossils.

DEPOSITIONAL SETTING

The unit from which the specimens of *Harpactocarcinus* described herein were collected has variously been called the ''marls with crabs'' or the ''transition beds'' (Juračić, 1979; Tunis and Uchman, 1996; Bergant et al., 2003). These beds lie between the foraminiferal (*Nummulites–Orthophragmina*) limestones, the platformal sediments, and the flysch deposits, the basin sediments, of the Istrian Peninsula. Most of the specimens of *Harpactocarcinus* and *Harpactoxanthopsis* recovered from the ''marls with crabs'' are corpses, because they retain the ventral portion of the carapace as well as poorly preserved appendages; thus, we can infer that the crabs were living in the described environments, and were not transported into the environment as buoyant molts of the carapace.

The ''marls with crabs'' have been assigned a lower middle Eocene, specifically middle Lutetian, age in the Floričići region (Juračić, 1979), from which we collected specimens of *Harpactocarcinus* (Drobne et al., 1979; Pavlovec et al., 1991; Ćosović and Drobne, 1998). Subsequently, an early Lutetian age was assigned to the ''marls with crabs'' in the regions of Buzet and Roč (Pavlovec and Pavšič, 1986) at localities from which we also collected specimens of *Harpactocarcinus*. Bergant et al. (2003) assigned a middle Lutetian age for the sediments in the Pazin Basin, which encompasses central to northeastern Istria. The Gračišče, Slovenia, sediments, from which we collected additional specimens of *Harpactocarcinus*, belong to the Brkini flysch complex (Šavrin Littoral Basin) and are of early Eocene (Ypresian) age according to the Geological Map, Sheet Trieste 1:100,000 (Pleničar et al., 1973), or are Lutetian (Pavlovec and Pavšič, 1986; Pavšič and Peckmann, 1996). Our analyses of sediments collected with specimens of *Harpactocarcinus* confirm the age differences between the Gračišče, Slovenia, and Floričići, Croatia, samples and those from Buzet-Roč, Croatia. The depth of deposition of these ''marls with crabs'' is estimated to have been from 60 to 100 m in the lower ''marls with crabs,'' deepening to up to 1,000 m in the upper part of the ''marls with crabs'' (Juračić, 1979).

The Gračišče packstones contain a rich foraminiferal assemblage, composed of larger and planktonic foraminifera along with authigenic glauconite (foraminiferan identifications after Toumarkine and Luterbacher, 1985; Less, 1987). Larger foraminifera assemblages with flat nummulitids, discocyclinids such as *Discocyclina dispansa* (Sowerby, 1840) and *D. archiaci* (Schlumberger, 1903), and operculinids are characteristic of low-energy, lower photic conditions. The planktonic foraminifera *Morozovella lehneri* (Cushman and Jarvis, 1929) and ''*Globigerinatheka*'' *senni* (Beckmann, 1953) are typical of the P-11 Biozone (sensu Berggren et al., 1995) of Lutetian age. These sediments were deposited in a quiet, open-marine, outer ramp setting with a significant pelagic influence, but that was shallow enough to support larger foraminifera in the lower photic zone. The presence of glauconite indicates deeper water and low sedimentation rates, with less oxygenated conditions (Odin and Matter, 1981).

The Buzet sample is composed of packstones in which larger foraminifera outnumber the planktonic ones, and glauconite grains are present in significant quantity. Planktonic foraminifera are present which are typical of the biostratigraphic zone P-11 (s. Berggren et al., 1995) of middle Lutetian age, including *Globigerinatheka mexicana* (Cushman, 1925), *Turborotalia frontosa* (Subbotina, 1953), *Turborotalia possagnoensis* (Toumarkine and Bolli, 1970), and *Subbotina inaequispira* (Subbotina, 1953). Larger foraminifera are well preserved and discocyclinids dominate,

TABLE 1—Fossil decapods previously reported from Istria and localities in Croatia other than Istria.

Decapod taxon	Localities	References
Achelous krambergeri Bittner, 1893	Croatia	Bittner, 1893
Calappa sp. Weber, 1795	Istria	Toniolo, 1909
Harpactoxanthopsis quadrilobatus (Desmarest, 1822)	Istria, Croatia	Bittner, 1883; Toniolo, 1909; Vogl, 1912 (Drvenik); Tarlao, 2000; Mikuž, 2002
Harpactocarcinus punctulatus (Desmarest, 1822)	Istria	Bittner, 1883; Toniolo, 1909
Harpactoxanthopsis souverbiei (A. Milne Edwards, 1862)	Istria	Toniolo, 1909
Lophoranina marestiana (König, 1825)	Istria	Bittner, 1883
Mioplax socialis Bittner, 1884	Croatia	Bittner, 1884
Neptunus radobajanus Bittner, 1884	Croatia	Bittner, 1884
Neptunus stenaspis Bittner, 1884	Croatia	Bittner, 1884

including *Discocyclina radians* (d'Archiac, 1850). Their abundance implies an open marine setting with winter water temperatures greater than 16°C (Hollaus and Hottinger, 1998). The depth is recognized as that of the lower photic zone, the reproductive depth for planktonic foraminifera. During Eocene time, when the studied area was located around 35°N paleolatitude (Butterlin et al., 1993a, 1993b), the estimated depth of the euphotic zone was about 100 m in clear water with no terrestrial input. This is suggested by the presence of glauconite grains. Oligotrophic conditions are inferred because of the presence of larger foraminifera.

The Floričići packstones contain rich planktonic foraminiferal associations. Fragments of discocyclinids are scattered throughout the micritic matrix. The foraminifera are typical of the middle Lutetian (P-12 Biozone, s. Berggren et al., 1995), including *Morozovella lehneri*, *Dentoglobigerina yeguaensis* (Weinzierl and Applin, 1929), and *Turborotalia frontosa*. The foraminifera collected by Juračić (1979), at the site of our collection, allow us to estimate that the depth was between 140 and 600 m, using the van der Zwaan et al. (1990) method.

COLLECTING LOCALITIES

Waypoint 42: near the village of Floričići, Istria, Croatia, lat. N 45°11′56.1″, long. E 14°3′27.2″, 2 km north from the town of Pićan.

Waypoint 44: near Buzet, Istria, Croatia, lat. N 45°23′52.4″, long. E 13°59′41.6″, cut-road on the eastern gateway to Buzet town.

Waypoint 46: near Gračišče village, Istria, Slovenia, lat. N 45°30′22.8″, long. E 14°1′59.2″, along the road between Gračišče-Kubed.

TABLE 2—Several localities for decapods in Istria, listed by Toniolo (1909), which are compiled with their modern names and location information.

Toniolo locality name	Modern locality name
Lesischina	Lesičina, village on the road Buzet-Roč, Croatia, 3 km southwest from Lupoglav
Cotle	Kotli, near Hum, Croatia; Hum is purportedly the world's smallest town; Kotli village is situated in the vicinity of the Roč-Hum road
Semi	Semic, a small village near Buzet, Croatia
Sergo	Crni kal, in Slovenia near the border with Italy
Rujavac	Unknown
Zulic	Problematic: there are two sites with this name. One is near Vizinada, and the other is near Waypoint 42 (Čepić Polje), both in Croatia
Torr. Baredine	Unknown; there is a Baredine cove, close to Poreč town, in Cretaceous rocks

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily XANTHOIDEA MacLeay, 1838
Family ZANTHOPSIDAE Via, 1959

Included genera.—*Harpactocarcinus* A. Milne Edwards, 1862; *Harpactoxanthopsis* Via, 1959; *Martinetta* Blow and Manning, 1997; *Neozanthopsis* Schweitzer, 2003; *Zanthopsis* McCoy, 1849.

Discussion.—Schweitzer (2003) raised Via's (1959) Zanthopsinae to family status and reevaluated all species previously referred to *Zanthopsis* and *Harpactocarcinus*. Therein are diagnoses for the family and the various genera it contains.

Genus HARPACTOCARCINUS A. Milne Edwards, 1862

Harpactocarcinus A. MILNE EDWARDS, 1862, p. 64, pls. 3–6, 8–10.

Type species.—*Cancer punctulatus* Desmarest, 1822 (=*Harpactocarcinus macrodactylus* A. Milne Edwards, 1862).

Other species.—*Harpactocarcinus achalzicus* Bittner, 1882; *H. istriensis* Bachmayer and Nosan, 1959; *H. jacquoti* A. Milne Edwards, 1865; *H. ovalis* A. Milne Edwards, 1862; *H. rotundatus* A. Milne Edwards, 1862.

Diagnosis.—See Schweitzer, 2003.

HARPACTOCARCINUS ISTRIENSIS Bachmayer and Nosan, 1959 new status

Figure 2

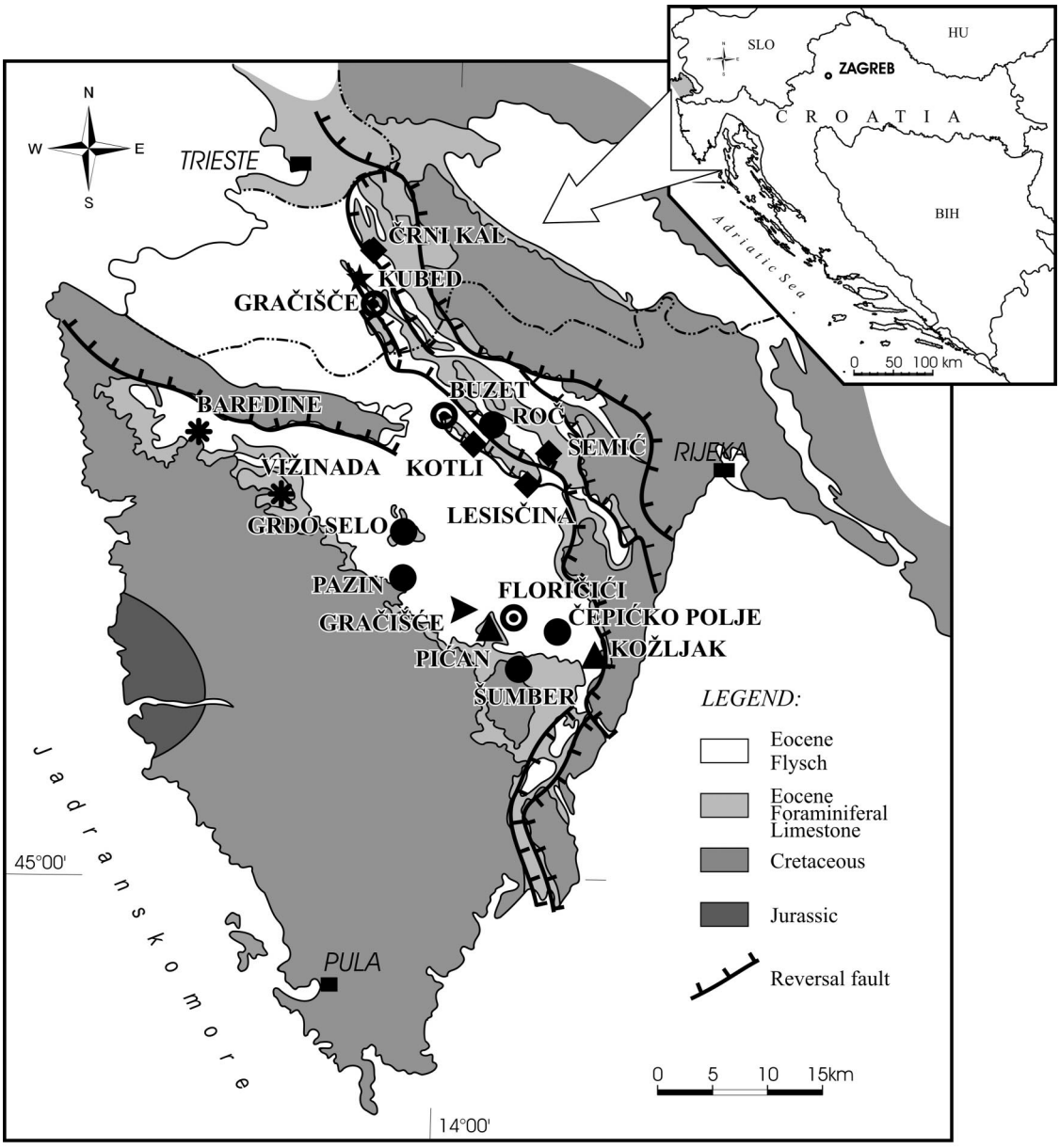
Harpactocarcinus punctulatus istriensis BACHMAYER AND NOSAN, 1959, p. 82, figs. 1, 2.

Diagnosis.—Carapace length about 80% width, widest about two-thirds the distance posteriorly on carapace; front projected beyond orbits, not obviously lobed; orbits deep, deepest laterally, outer-orbital spine extending slightly beyond front; anterolateral margin weakly convex, with about 13 small, sharp spines.

Description.—Carapace wider than long, L/W about 80%, narrowing considerably posteriorly, widest about two-thirds the distance posteriorly on carapace; moderately vaulted longitudinally, especially posteriorly, and moderately vaulted transversely.

Front projected beyond orbits, appearing to narrow distally, frontal width about one-quarter maximum carapace width. Orbits deep for genus, circular, rimmed, deepest on outer edges; outer-orbital spine projected slightly beyond front, triangular, directed forward; fronto-orbital width about half maximum carapace width.

Anterolateral margin weakly convex, with about 13 small, sharp spines; posterolateral margin nearly straight, thickened; posterior margin narrow, straight, about 28% maximum carapace width.



● Stache, 1889
◆ Toniolo, 1909
✱ uncertain Toniolo's sites, 1909
▲ Salopek, 1954
★ Bachmayer and Nosan, 1959
▶ Pavlovec and Pavšič, 1986; Mikuž, 2002
Tarlao, 2000
⊙ this paper

FIGURE 1—Geologic map of Istria, with decapod collecting localities marked. Collecting localities of various authors as well as those reported in this paper are designated by different symbols (see key). Map modified from the Basic Geologic Map of Former Yugoslavia, 1:500,000, issued in Belgrade by the Federal Geological Survey (1970).

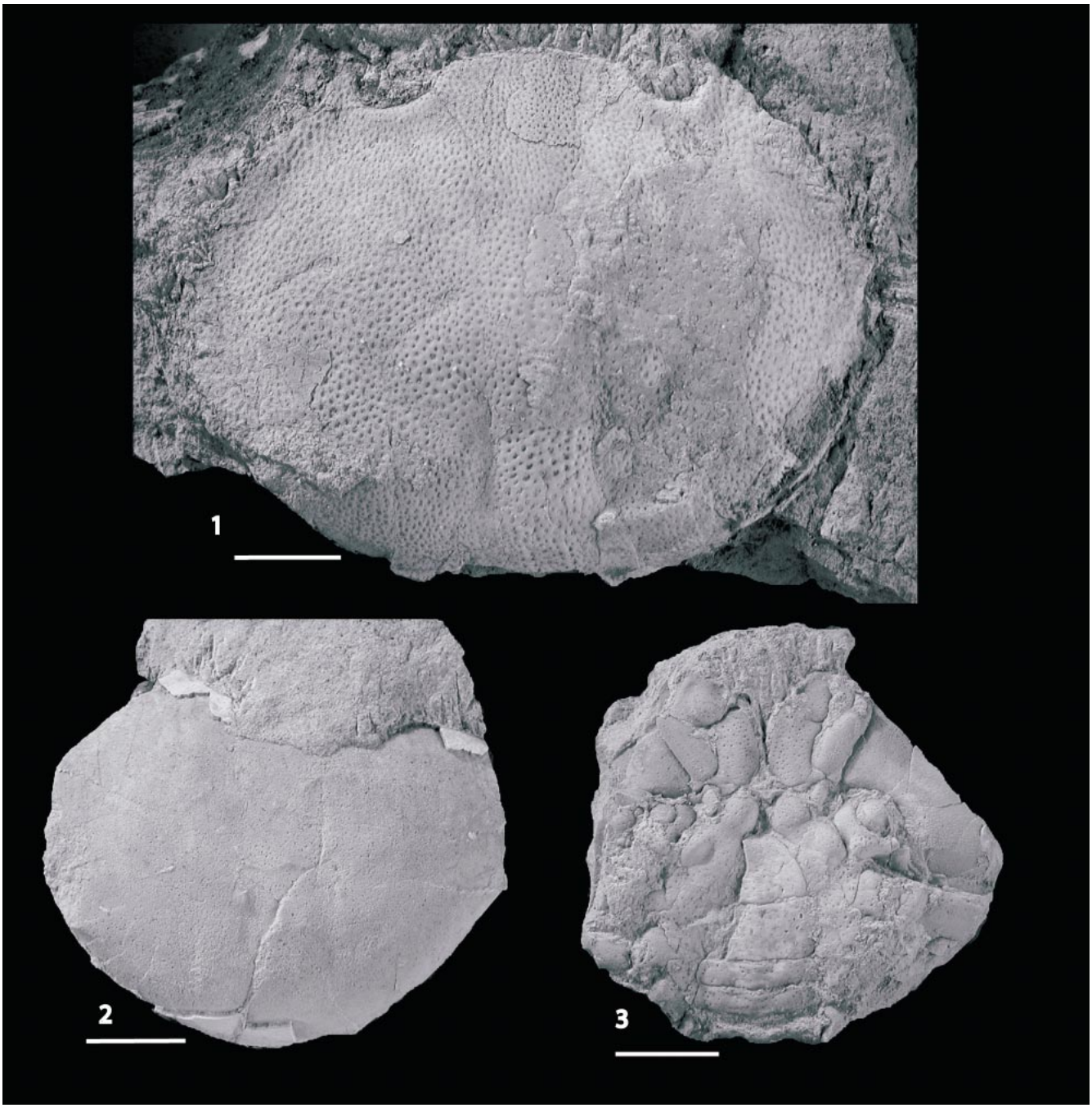


FIGURE *2*—*Harpactocarcinus istriensis* Bachmayer and Nosan, 1959 new status. *1*, Dorsal carapace, note produced outer-orbital angles, specimen 010703; *2*, dorsal carapace with preserved posterior margin, specimen 020703; *3*, sternum and abdomen of immature female, specimen 030703. Scale bars = 1 cm.

Carapace surface densely punctate; regions ill-defined; protogastric and epibranchial regions weakly swollen; branchiocardiac groove outlining margins of urogastric and anteriormost cardiac region very distinct.

Sternum of immature female longer than wide, width about 70% length, widest at position of episternites of sternite 4; sternites 1 and 2 fused, suture between sternites 2 and 3 continuous; sternites 3 and 4 fused, suture between them a shallow groove oriented at moderate angle; very large knobs on sternite 4 near bases of coxae of pereiopod 1, possibly episternites of sternite 3 fused to sternite 4; deep, short groove extending anteriorly onto sternite 3 from sterno-abdominal cavity; suture between sternites 4 and 5 at low angle; sternites 5 and 6 narrow, with episternal projections; sternite 7 barely visible; sternite 8 not visible.

Abdomen of immature female with straight sides, somites 4–6 appear to be fused, telson long, bluntly triangular.

Surface of third maxillipeds punctate; first pereiopods quite large.

Type.—The specimen illustrated by Bachmayer and Nosan (1959) is the holotype, Inv. Nr. 2211, deposited in the Department of Geology, Faculty of Natural Sciences and Engineering, Ljubljana, Slovenia.

Other material examined.—Specimens 010703–130703, deposited in the collections of the Department of Geology and Paleontology, University of Zagreb, Croatia.

Occurrence.—The specimens illustrated here were collected from the ''crab marls,'' which are no younger than middle Eocene, based upon a middle Eocene age for the overlying flysch deposits (Magdalenić, 1972). Specimens 010703–070703 were collected from Waypoint 42; 090709 was collected from Waypoint 44; and 080703, 100703–130703 were collected from Waypoint 46.

Discussion.—Bachmayer and Nosan (1959) created a new subspecies, which they called a nov. var. (p. 81), *Harpactocarcinus punctulatus istriensis*, to accommodate specimens of *Harpactocarcinus* collected in Istria, Croatia. Herein we elevate the subspecies to species level because the Istrian material differs significantly from *H. punctulatus* Desmarest, 1822, and all other species within the genus. Species of *Harpactocarcinus* are differentiated based upon the length/width ratio of the carapace, the number of anterolateral spines, and the relative size of the front, orbits, and frontal and orbital spines. Neither the front nor the outer-orbital spines in *H. punctulatus* or any other species in the genus are projected beyond the orbits, as seen in the Istrian material. In a genus with such uniform morphology, this is a major difference. The orbits of *H. rotundatus* are much smaller than in the Istrian material and they lack outer-orbital spines as seen in *H. istriensis*. *Harpactocarcinus* ovalis is much more ovate in shape than the Istrian material and has broader orbits and smaller outer-orbital spines than *H. istriensis*.

Bachmayer and Nosan (1959, p. 83) commented that the material they referred to *Harpactocarcinus punctulatus istriensis* was similar to members of both *Harpactocarcinus* and *Harpactoxanthopsis*. Via (1959) and Schweitzer (2003) discussed the differences between these two genera, the major difference being that species of *Harpactoxanthopsis* possess four well-developed anterolateral spines and a very distinctly quadrilobed front, while species of *Harpactocarcinus* have between 8 and 15 small, sharp anterolateral spines and a weakly quadrilobed front. The new material, based upon its possession of 13 small, sharp anterolateral spines and an indistinctly lobed front, is clearly a member of *Harpactocarcinus*. Species of *Harpactoxanthopsis* have also been reported from Istria (Tarlao, 2000); those specimens are clearly referrable to *Harpactoxanthopsis* due to their possession of four large, distinct anterolateral spines. Mikuž (2002) reported *Harpactoxanthopsis quadrilobata* (Desmarest, 1822) from near Gračišče, Croatia, but the specimens lack well-preserved anterolateral margins, making it difficult to determine if the specimens are referrable to *Harpactocarcinus* or *Harpactoxanthopsis*.

SIGNIFICANCE

Previously described species of the genus are known from sites in Europe; thus, the occurrence herein does not broaden the geographic age. However, based upon our paleoenvironmental analysis, we know that *Harpactocarcinus istriensis* n. status preferred clear water in open-marine, middle to outer continental shelf settings below fair-weather wave base. This is the first quantitative analysis of the paleoenvironmental preference of a member of the Zanthopsidae Via, 1959. A review of the literature pertaining to species within the genera referred to the Zanthopsidae supports this paleoenvironmental analysis qualitatively.

Species of *Zanthopsis* are reported in the literature from the London Clay (Bell, 1858), deposited in outer shelf conditions of between 20 and 150 m (Taylor, 1978); glauconitic marls of Texas (Stenzel, 1934; Wilmarth, 1957); nummulitic marls (Van Straelen, 1927); and active marginal, slope sediments (Rathbun, 1926; Feldmann et al., 1991). *Harpactocarcinus* spp. are known from nummulitic beds in France, Hungary, Italy, Spain, and Switzerland (A. Milne Edwards, 1862, 1865; Lőrenthey, 1898; Van Straelen, 1927) and the ''marls with crabs'' in Croatia. Species of *Harpactoxanthopsis* are described from the ''marls with crabs'' of Croatia (Tarlao, 2000); nummulitic beds in France and Hungary (A. Milne Edwards, 1862; Lőrenthey, 1898); bryozoan marls in Hungary (Lőrenthey, 1898); and foraminiferan-rich beds in Spain (Via, 1959). *Martinetta* is known from the Santee Limestone, a marly unit in South Carolina, USA (Wilmarth, 1957; Blow and Manning, 1997). *Neozanthopsis* spp. are reported from glauconitic shales and marls of the Gulf Coastal Plain, USA (Stenzel, 1934; Schweitzer, 2003).

There are many commonalities in these paleoenvironmental descriptions for members of the Zanthopsidae. Members of the family seem to have preferred environments in which glauconite accumulated. The presence of larger, benthic foraminifera is very clearly a common factor for many species as is their occurrence in marls. All of this, along with the qualitative analysis above, suggests that the Zanthopsidae preferred open, clear, marine shelf conditions, below fair-weather wave base. The interpretation of such a tightly constrained paleoecological preference for an extinct decapod group has not before been possible.

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