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New crabs (Decapoda: Brachyura: Prosopidae) from Jurassic (Oxfordian) sponge bioherms of Dobrogea, Romania

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Abstract

A previously undescribed fauna of primitive brachyurans of the family Prosopidae is reported from sponge bioherms in eastern Romania. One new species, *Cycloprosopon dobrogea*, and several other forms, constitute the brachyuran fauna. The sponge bioherms, which attain a height of 30 meters, have yielded an abundant, but not overly diverse, array of benthic invertebrates. Some of the brachyuran specimens bear epibionts, unusual in the fossil record of the Decapoda. The constitution of several genera within the Prosopidae is herein summarized in order to facilitate further work on the family within the context of modern systematic methods.

Key words: Decapoda, Brachyura, Prosopidae, Jurassic, Oxfordian, Romania, sponge bioherm

Introduction

The purpose of the present work is to document a previously undescribed fauna of primitive crabs of the family Prosopidae that are a significant part of a sponge bioherm biota in eastern Romania. The decapod fauna consists of several taxa arrayed within three genera. The genus *Goniodromites* dominates the decapod fauna. This genus is widespread in the Jurassic faunas of Europe and constitutes one of the geologically oldest genera of crabs.

The various genera within the family Prosopidae von Meyer, 1860, have received little systematic attention in recent years, with a few notable exceptions (Collins and Wierzbowski, 1985; Müller *et al*., 2000). Provided herein is a summary of the work to date on the subfamily Goniodromitinae Beurlen, 1932, of this family, including some translations of the original work in German, to facilitate ongoing investigation into this basal group within the Brachyura.

Lithostratigraphy and Geologic Setting

The Jurassic formations from Central Dobrogea (SE Romania) are represented by Middle Jurassic (Upper Bathonian–Callovian) and Upper Jurassic (Oxfordian–Kimmeridgian) deposits. Central Dobrogea is a sector of the Moesian Platform; a sector that is bounded by the Peceneaga–Camena Fault on the North and the Capidava–Ovidiu Fault on the South (Fig. 1). The lithostratigraphy of the Jurassic deposits from Central Dobrogea is represented by three units: Tichilesti Formation, Gura Dobrogei Formation and Casimcea Formation (Bărbulescu *in* Dragastan *et al*., 1998). The Jurassic deposits represent the lowest part of the sedimentary cover that is deposited over the basement (Vendian–Lower Cambrian age, so called “green schists”). Even though generally the Jurassic rocks are covered by a thick loess layer and the outcrops have small dimensions, there are some areas with good outcrops such as the Cheia Valley that represent the studied section in the present paper.

Exposures of Oxfordian (lower Upper Jurassic) carbonate rocks in Central Dobrogea record a remarkable sponge-algal biostromal/bioherm complex and its associated fauna. The area of the best exposure of these deposits is situated near the village of Cheia and is dissected by the Cheia River (Fig. 1). The deposits are included within the Visterna Member that represents the lower part of the Casimcea Formation. The Oxfordian–Kimmeridgian age of the Casimcea Formation is documented by ammonite faunas (especially in western Central Dobrogea) (Anastasiu, 1898; Simionescu, 1907, 1910; Patrulius and Orghidan, 1964; Bărbulescu, 1969, 1970, 1974, 1979; Chiriac *et al*., 1977; Bărbulescu in Dragastan *et al*., 1998). The biostratigraphy and the detailed paleoecological observations of the Visterna Member were outlined by Bărbulescu (1961, 1969, 1971a, b, 1972, 1974, 1979; Bărbalescu *in* Dragastan *et al*., 1998). Detailed biofacies analysis was defined by Herrmann (1994, 1996), and biozonation of the formation was largely defined by Bărbulescu (*in* Dragastan *et al*., 1998).

The development of the sponge-algal facies was initiated during

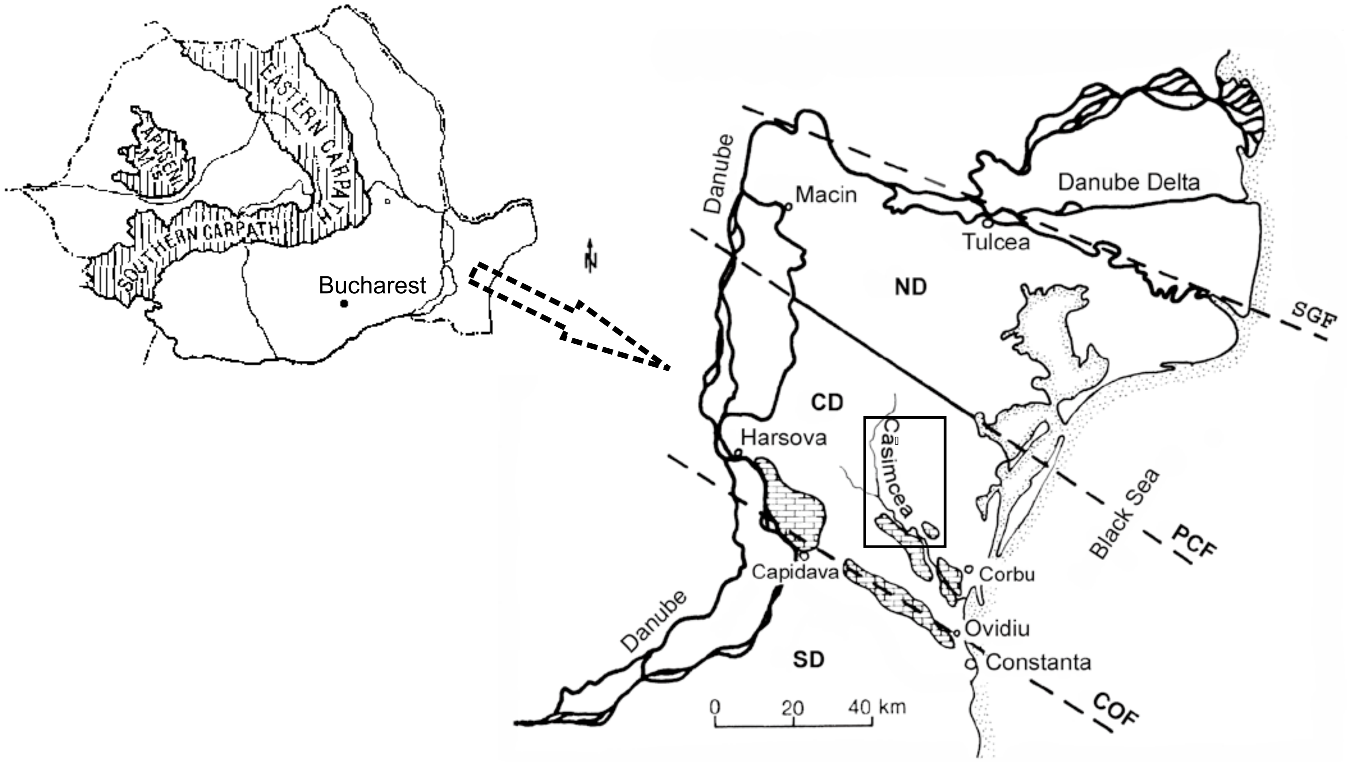

Fig. 1. Location map of the studied area. Brick pattern in area enlarged at right indicates outcrops of coral and sponge bioherm limestones; box indicates location of sponge bioherm outcrops in Casimcea Valley. CD, Central Dobrogea; ND, North Dobrogea Orogen; SD, South Dobrogea; SGF, Sfântu Gheorghe Fault; PCF, Peceneaga–Camena Fault; COF, Capidava–Ovidiu Fault (Modified from Herrmann, 1996).

the Lower Oxfordian in a few local places in Central Dobrogea (Harsova, Galbiori, Crucea, Casimcea Valley) and continued until the end of the Upper Oxfordian. During this interval of time, the sponge-algal facies occupied a very large area in the western and also in the eastern part of Central Dobrogea, being the most developed organogenic biofacies from Dobrogea (Bărbulescu in Dragastan *et al*., 1998). The Visterna Member was divided into two complexes: the lower biostromal complex and the upper biohermal complex (Drăgănescu, 1976), both of them comprised of successive generations of platy sponges and microbial carbonatic crusts which confers a pseudo-stratified aspect to these deposits.

The most spectacular geomorphologic aspect is shown by the individual cylindrical sponge–algal bioherms, with diameters of approximately 30 m, standing approximately 25 m above the valley floor (Fig. 2). Each bioherm has a hollow core filled by a limonitic carbonate breccia, and each is separated from adjacent bioherms by flanking, well-bedded inter-bioherm talus. The cylindrical bioherm masses are thought to have formed over subtle elevations on the seafloor and, once established, to have grown vertically. Although there is little physical evidence to document the elevation of the rings above the seafloor during their growth, Herrmann (1996) speculated that they were probably low-relief features. Because each cylindrical bioherm attains a diameter of approximately 30 m, this suggests that some biotic or hydraulic dynamic may have governed the size of the build-ups. It is possible that this was the optimal size to provide adequate circulation of water to sustain the bioherm-building organisms.

The sponge–algal biohermal and biostromal limestones are comprised of about 80% siliceous sponges and microbialiths. The sponges are representatives of the class Demospongea and the microbialiths are produced by cyanobacteria (Drăgănescu, 1976; Gaillard, 1983; Herrmann, 1996). The cylindrical bioherms formed near the distal margin of a carbonate ramp in water depths below normal wave base. Sponge biostromes were formed seaward and coral patch reefs and lagoonal deposits were formed landward of the sponge–algal bioherms.

The benthic organisms other than sponges are represented by several invertebrate groups (Table 1). In approximate order of abundance, serpulid worms *Serpula* (*Cycloserpula*), *S.* (*Dorsoserpula*), and *S.* (*Tetraserpula*)) are most abundant. They are found on the lower surfaces of the sponges and on the upper part of the algal crusts. Other components include bryozoans; stromatoporoids; cidarioid and irregular echinoids; crinoids; the cemented craniacean brachiopods *Lacunosella*, *Moeschia*, and *Argovithyris*; terebratulid, rhynchonellid, and thecideiid brachiopods; and rare pelecypods, gastropods, and cephalopods including ammonites and belemnites. Neither the crabs nor the belemnites have been reported previously. The associated benthic faunal elements tend to be small, probably occupying niches within the bioherms, and represent a biocoenosis. Diversity is low for each group of organisms. Abundance of specimens is uniform and moderate in all facies. The architectural framework of the sponge-

Fig. 2. Panoramic view of the cylindrical sponge reefs of the Cheia Valley, Central Dobrogea, Romania, summer 2005. Note the Dacia cars for scale.

algal bioherm complex is uniquely preserved so that the composition and distribution of benthic organisms within the complex can be clearly delineated.

The decapod specimens collected from the bioherms of the Cheia River Valley are all small and are ideally adapted to seek shelter in the cryptic habitats within the reef complex. The large number of species within one brachyuran family suggests that increase in diversity and niche partitioning occurred within the limited number of genera of Jurassic crabs rather than between genera.

Localities

All of the localities are in the Cheia Valley, not far from the town of Mihail Kogalniceanu, in the Dobrogea region of eastern-most Romania in the lower to upper Oxfordian Casimcea Formation.

WP 125: lat. 44°30´03.5˝ N, long. 28°25´26.2˝ E, from the inner core of the sponge bioherm.

WP 126: lat. 44°30´01.4˝ N, long. 28°25´33.7˝ E, in the sponge bioherm itself.

WP 127: lat. 44°30´08.9˝ N, long. 28°25´30.9˝ E, from inter-bioherm talus.

Institutional Abbreviations

CM – Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

LBPIIIart – Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Romania

MSB – Museu Geologico del Seminari de Barcelona, Spain

Systematic Paleontology

Family Prosopidae von Meyer, 1860

Subfamily Goniodromitinae Beurlen, 1932

Genus *Pithonoton* von Meyer, 1842

Ogydromites A. Milne Edwards, 1865. This synonymy is historical (Glaessner, 1929; Wright and Collins, 1972) and is listed for the sake of completeness. It has not been confirmed by the authors. *Ogydromites* may in fact be a distinct genus (Glaessner, 1969).

Type species: *Pithonoton marginatum* von Meyer, 1842.

Other referred species: *Pithonoton aequilatum* (von Meyer, 1860) as *Prosopon* von Meyer, 1835; *P. angustum* Reuss, 1859; *P. bouvieri* Van Straelen, 1944; *P. campichei* (Tribolet, 1874), as *Prosopon; P. cenomanense* Wright and Collins, 1972; *P. elongatum* (von Meyer, 1860) as *Prosopon*; *P. hungaricum* Lőrenthey *in* Lőrenthey and Beurlen, 1929; *P. hypocrita* Étallon, 1861; *P. inflatum* Collins and Karasawa, 1993; *P. insigne* von Meyer, 1860; *P. katholickyi* (Remeš, 1895), as *Prosopon; P. laevimarginatum* Lőrenthey *in* Lőrenthey and Beurlen, 1929; *P. lingulatum* von Meyer, 1860; *P. meyeri* Étallon, 1859; *P. moutieri* (Hée, 1924), as *Prosopon*; *P. nitidus* (A. Milne Edwards, 1865), as *Ogydromites* H. Milne Edwards, 1837; *P. obtusum* (von Meyer, 1860), as *Prosopon*; *P. planum* Van Straelen, 1936; *P. polyphemi* (Gemmellaro, 1870), as *Prosopon*; *P. quadratum* (Étallon, 1857), as *Prosopon*; *P. renevieri* (Tribolet, 1876), as *Prosopon*; *P. richardsoni* (Woodward, 1907), as *Prosopon*; *P. rostratum* von Meyer, 1842; *P. rusticum* Patrulius, 1966; *P. simplex* (von Meyer, 1840), as *Prosopon*; *Pithonoton* sp. *in* Donovan (1962); *Pithonoton* sp. *in* Wright and

Table 1. List of species of benthic organisms arrange in approximate order of abundance (authors observations and other data from Bărbulescu in Dragastan *et al*., 1998).

Group	Taxon
Sponges (80% of the assemblage)	*Platychonia schlotheimi* (Münster) *Hyalotragos patella* (Goldfuss) *Hyalotragos pezizoides* (Goldfuss) *Tremadictyon phyloideum* Antonescu *Stauroderma lochensis* (Quenstedt) *Trochobolus texatus* (Goldfuss) *Laochaetis parallela* (Goldfuss) *Sporadophile* sp. *Paracraticularia* sp. *Cylindrophyma* sp. *Eudea clavata* Lamouroux
Encrusting sponges	*Neuropora spinulosa* (Lamouroux)
Serpulid Worms	*Serpula* (*Cycloserpula*) *gordialis* (Schlotheim) *Serpula* (*Cycloserpula*) *munsteri* Parsch *Serpula* (*Dorsoserpula*) *lumbricalis* (Schlotheim) *Serpula* (*Cycloserpula*) *flaccida* Goldfuss *Serpula* (*Tetraserpula*) *tricarinata* Goldfuss
Brachiopods	*Rioultina virdunensis* Buvignier *Crania* sp. *Craniscus* sp. *Ismenia* sp. *Trigonellina intercostata* (Quenstedt) *Lacunosella* sp. *Lacunosella trilobateformis* Wisniewska *Lacunosella arolica* (Oppel) *Moeschia alata* (Rollet) *Argovithyris birmensdorfensis* (Moesch) *Zeillerina delmontana* (Oppel)
Bryozoans	*Stomatopora corallina* (d'Orbigny) *Ceriocava corymbosa* (Lamouroux) *Plagioecia* sp.
Echinoids	*Collyrites* sp. Numerous Cidaridae plates and spines
Crinoids	*Millecrinus* sp.
Pelecypods	Indeterminable specimens from: Ostreoida, Pectinidae (?*Camptochlamys* sp.), Dimyidae (?*Atreta* sp.)

Collins (1972). List after Glaessner (1929, 1933).

Diagnosis: Carapace longer than wide, carapace width 75–80 percent maximum length, widest just anterior to intersection of cervical groove with lateral margin, carapace narrowing posteriorly from position of maximum width or rectangular; carapace moderately vaulted transversely and longitudinally. Carapace surface granular, granules larger posteriorly.

Front short, bifid, each bifurcation blunt and rounded, merging smoothly with orbits, orbits extending in concave arc to outer-orbital angle produced into a spine, orbital margin at about 40 – 45° angle to axis; lateral margin entire.

Mesogastric region most strongly defined posteriorly, ovate, defined posteriorly by deep, well-developed cervical groove, mesogastric region sometimes nearly completely lacking entire anterior process but with weakly defined fragment of process anteriorly, just posterior to the position of the rostrum or with entire anterior process weakly defined, anterior portion of mesogastric region sometimes bounded by weak, small epigastric swellings; outer segment of cervical groove at about 80–85° angle to axis.

Metagastric and urogastric regions weakly but noticeably differentiated; metagastric region separated from urogastric region by shallow, sinuous post-cervical groove; urogastric region very narrow, depressed below level of other axial regions. Cardiac region inflated, ornamented with tubercles which are sometimes arranged into rows on posterior portion of carapace, laterally and posteriorly defined by deep, well-defined, continuous branchio-cardiac groove, sometimes more weakly defined than cervical groove. Remainder of carapace regions not well-differentiated, branchial regions weakly inflated and often seen with bopyrid swellings.

Posterior margin weakly concave, rimmed.

Discussion: *Pithonoton* was originally erected in 1842 by von

Meyer for two species of *Prosopon*, *Prosopon marginatum* and *Prosopon rostratum*. Subsequently, *Pithonoton marginatum* has been considered as the type species for *Pithonoton* (Glaessner, 1929; 1969). The original material upon which *Pithonoton marginatum* was based was broken, so that the front and orbits were not preserved (von Meyer, 1842), and the description was therefore quite incomplete. Subsequently, von Meyer (1860) described additional, more complete material which he referred to the species, which showed a range of sizes and documented allometric growth. In the years after this, specimens from all over Europe have been referred to *Pithonoton marginatum*, some appearing to be similar to von Meyer's material and some not (Gemmellaro, 1870; Moericke, 1889; Remeš, 1895, 1905; Lőrenthey and Beurlen, 1929; Patrulius, 1966; Müller *et al*., 2000; Garassino *et al*., 2005). In addition, numerous species have since been referred to *Pithonoton*, some of which differ substantially from *P. marginatum* (see, for example, illustrations *in* Müller *et al*., 2000) and resulting in *Pithonoton* embracing a broad morphological range. Unfortunately, the location of von Meyer's type and 1860 material is unknown. Thus, we have based our diagnosis on von Meyer's (1842, 1860) descriptions (translated below) and illustrations, in order to best reflect the original sense of the genus.

In addition to embracing a broad morphological range itself, *Pithonoton* has been considered to embrace three subgenera, *Pithonoton* (*Pithonoton*), *P.* (*Cycloprosopon*), and *P.* (*Goniodromites*) (Glaessner, 1969). Glaessner (1929) was apparently the first to consider *Goniodromites* Reuss, 1859, and *Pithonoton* as subgenera of *Pithonoton*. *Pithonoton* (*Pithonoton*) apparently was construed to embrace species allied with *P. marginatum*, having equally strong branchiocardiac and cervical grooves (Glaessner, 1969). *Goniodromites* was originally named as an independent genus (Reuss, 1859) but was later considered as similar to *Pithonoton* (*Pithonoton*) but having a weaker branchiocardiac than cervical groove (Glaessner, 1969). *Pithonoton* (*Cycloprosopon*) was originally designated as a subgenus of *Pithonoton* (Lőrenthey *in* Lőrenthey and Beurlen, 1929) and that designation has been maintained until this time.

Examination of the original descriptions and illustrations of all three of these subgenera of *Pithonoton* indicates that each should be considered to be independent genera. *Cycloprosopon* was described to embrace species with a rounded, smooth carapace; a well-defined cervical groove; and lacking a rostrum (Lőrenthey *in* Lőrenthey and Beurlen, 1929). It has been maintained as a subgenus of *Pithonoton* ever since its original description, despite being quite different in many regards from *Pithonoton* (*Pithonoton*). *Pithonoton* possesses a longer than wide, granular carapace; an outer-orbital spine; a well-defined posterior portion of the mesogastric region; differentiated axial regions including the mesogastric, metagastric, urogastric, and cardiac regions; and well-developed cervical and branchio cardiac grooves. *Cycloprosopon* possesses an equant carapace and lacks defined axial regions except the mesogastric at times, an outer-orbital spine, and a branchiocardiac groove altogether or has only a very poorly developed one. Thus, we raise *Cycloprosopon* to genus level.

Differentiation of *Goniodromites* Reuss, 1859, from *Pithonoton sensu stricto* is somewhat more difficult but can be achieved (Table 2). Species of *Pithonoton* are characterized by exhibiting a smooth orbital margin and posterior dorsal carapace ornamentation usually consisting of tubercles, whereas species of *Goniodromites* can have a serrate orbital margin and always have scabrous posterior dorsal carapace ornamentation, consisting of small tubercles connected in rows. The lateral margins in species of *Pithonoton* are entire, whereas those of *Goniodromites* spp. are ornamented with lateral spines. The dorsal carapace of species of *Pithonoton* narrows weakly posteriorly or is rectangular, but species of *Goniodromites* narrow considerably both anteriorly and posteriorly. Species of *Goniodromites* are as long as wide, wider than long, or longer than

Table 2. Characteristics differentiating species of *Pithonoton* and *Goniodromites.*

Pithonoton	*Goniodromites*
Differences	
smooth orbital margin	may have a serrated orbital margin
usually tubercles or warts on dorsal carapace	rows of forward directed prominences on dorsal carapace
anterolateral margin entire	anterolateral margin with spines
narrows weakly posteriorly or rectangular	narrows strongly posteriorly
W/L = 0.75–0.80	W/L = 0.85–1.05
40–45° angle of orbit to axis	45–50° angle of orbit to axis
Similarities	
80–85° angle of cervical groove to axis	80–85° angle of cervical groove to axis
bilobed blunt front	bilobed blunt front
cervical and branchiocardiac grooves present and complete, branchiocardiac may be weaker	cervical and branchiocardiac grooves present and complete, branchiocardiac may be weaker
mesogastric region incompletely defined	mesogastric region incompletely defined
general arrangement of regions and grooves is same	

wide, with width to length ratios ranging from 0.85 to 1.05. By contrast, *Pithonoton* is always longer than wide, with the width measuring between 75 and 80 percent the length. The angle of the orbital margin with the axis of the animal measures between 40 and 45 degrees in *Pithonoton* and between 45 and 50 degrees in *Goniodromites*. The latter three characters create a very different overall dorsal carapace shape among species of the two genera and clearly separate them.

Alphonse Milne Edwards (1865) described a species, *Ogydromites nitidus*, from Neocomian rocks of France, and discussed the similarities of *Ogydromites* A. Milne Edwards, 1865, with *Pithonoton*, noting that *Ogydromites* had priority over *Pithonoton* as a genus name. Glaessner (1929) placed *O. nitidus* within *Pithonoton*, but interestingly, in his later work on Jurassic crabs (Glaessner, 1933), neither that species nor *Ogydromites* was mentioned. Van Straelen (1944) considered *Ogydromites* as a genus separate from *Pithonoton* but did not explain the points of differentiation between the two genera. Glaessner (1969, p. R485) regarded *Ogydromites* as a synonym of *Pithonoton* but did note that *Ogydromites* had "not been clearly diagnosed." Wright and Collins (1972) discussed the history of the name *Ogydromites*, which had been erected by H. Milne Edwards apparently as a *nomen nudum* in 1837 and later made available by A. Milne Edwards (1865), and they regarded it as a synonym of *Pithonoton*. Thus, it is clear that types of *Ogydromites* must be examined in order to determine if it is in fact synonymous with *Pithonoton*.

Herein, we provide a list of species that have historically been referred to *Pithonoton* and that have not been subsequently referred to other genera, based largely upon the work of Glaessner (1929, 1933) (Table 3). The number of species that should be embraced by *Pithonoton sensu stricto* has not been verified and the number of referred species has fluctuated widely over time. Glaessner (1929) referred 23 species, two of these questionably, to *Pithonoton* (*Pithonoton*), but only a few years later referred only ten species and an additional eight questionably to the genus and subgenus (Glaessner, 1933). In a much more recent work, Müller *et al*. (2000) reported that the genus embraced only thirteen species; this number apparently included those referred to all three subgenera, not just *Pithonoton* (*Pithonoton*).

A major problem in referring species to *Pithonoton* or other

Table 3. Species referred to *Pithonoton*, their age, and geographic occurrence. Most have not been verified; thus, they are simply arrayed alphabetically. [1]Data from Glaessner (1929).

Species	Age	Geographic Occurence
P. marginatum (type)	Tithonian[1] Latest Kimmeridgian (Garassino *et al*., 2005)	Germany[1], Garassino *et al*., 2005; ?Central Romania (Patrulius, 1966)
P. aequilatum	middle late Jurassic[1]	southern Germany[1]
P. angustum	middle late Jurassic[1]	eastern Czech Republic1, Germany[1]
P. campichei	Neocomian[1]	Switzerland
P. cenomaniense	Cenomanian (Wright and Collins, 1972)	England[1]
P. elongatum	middle late Jurassic[1]	southern Germany[1]
P. hungaricum	Tithonian[1]	Romania, formerly Hungary[1]
P. hypocrita	middle late Jurassic[1]	Switzerland[1]
P. inflatum	?Cenomanian–Campanian (Collins and Karasawa, 1993)	Japan
P. insigne	middle late Jurassic[1]	Germany[1]
P. katholickyi	Tithonian[1]	eastern Czech Republic[1]
P. laevimarginatum	Tithonian[1]	Romania, formerly Hungary[1]
P. lingulatum	middle late Jurassic[1]	southern Germany[1]
P. meyeri	middle late Jurassic[1]	France[1]
P. moutieri	middle middle Jurassic[1]	northern France[1]
P. nitidus	Neocomian (A. Milne Edwards, 1865)	France[1]
P. obtusum	middle late Jurassic[1]	Germany[1]
P. planum	Neocomian (Van Straelen, 1936)	France[1]
P. polyphemi	Tithonian[1]	Sicily[1]
P. quadratum	Oxfordian[1]	Switzerland[1], France[1]
P. renevieri	Neocomian[1]	Switzerland[1]
P. richardsoni	middle middle Jurassic[1] Bajocian (Withers, 1951)	England[1]
P. rostratum	late late Jurassic[1] Oxfordian[1] ?Bajocian[1]	Germany[1], France[1], Switzerland[1]
P. rusticum	Tithonian (Patrulius, 1966)	Central Romania (Patrulius, 1966)
P. simplex	lower upper Jurassic[1]	southern Germany[1]

closely related forms is that much of the nineteenth century type material cannot be located. Some of the original types were in private collections (G. Schweigert, pers. commun.), and other specimens were possibly destroyed during World War II. Thus, comparative study has been hampered considerably. Twentieth century workers have referred newly collected material to some of the species named during the nineteenth century, but at times it is unclear if the new material should truly be referred to that species, especially when collected from locations hundreds or thousands of kilometers away from the type locality. For example, *Goniodromites bidentatum* has been reported from the Jurassic of the eastern Czech Republic (Reuss, 1859, the location of the type); central Romania (Patrulius, 1966); and France (Müller *et al.*, 2000). It is not clear if the occurrences other than those at the Czech site are in fact referrable to the species. In our examination of descriptions and illustrations of species referred to *Pithonoton sensu lato* or even to *Pithonoton* (*Pithonoton*), we have found that the range of variation is untenable and that the genus must be subdivided. That work is ongoing.

***Pithonoton marginatum* von Meyer, 1842**

Description (translated from the original German [von Meyer, 1842], additions added in square brackets): The front portion of the left side of the cephalothorax of this animal and indeed all the way to the forward end is missing, so that the investigation is hampered. The width of the cephalothorax amounts to 0.006 [units for this measurement not given in the original] and its length appears to be the same. The maximum width lies near the front end of the middle main part [area of carapace between the cervical and branchiocardiac grooves], from which the cephalothorax becomes gradually narrower toward the anterior and toward the posterior, and indeed narrowing toward the anterior somewhat more rapidly on account of the shorter distance. Nevertheless the posterior narrowing compared to related forms is very clear.

The rear indentation for the reception of the abdomen is either not bordered, or only very finely bordered, especially in comparison with *Prosopon spinosum*; also it is proportionately less wide, and reminds us thereby of the Short-tailers [interpreted by us to mean primitive crabs with portions of the abdomen extending distally from the cephalothorax and visible in dorsal view].

In the vaulting of the dorsal carapace, this species is more similar to *Prosopon rostratum* and generally more closely related to it.

The front main part [portion of carapace anterior to cervical groove] is shorter than both others [sections of the cephalothorax] taken together. One distinction on it properly speaking [is] only a raised transverse oval posterior region [posterior portion of mesogastric region], from which probably no rostrum-like prolongation extends toward the front end of the cephalothorax. A small thin border surrounds the forward main part externally, which on the lateral side allows a clear spine to be observed. Behind the posterior region lies a pair of holes in the transverse [cervical] groove, which is, however, not very clearly expressed.

The middle main part [portion of carapace between cervical and branchiocardiac grooves] projects at a sharp angle into the posterior [main part, portion of carapace posterior to branchiocardiac groove], and expresses itself less by elevations than by two pairs of linear impressions. The impressions of the one pair lie right on the place where the middle main part extends into that which lies behind and opens up into the transverse groove. How this pair traverses on a short stretch of the middle main part from the beginning toward the posterior, so lies the possibly even shorter impressions of the second pair on the place where the former takes its beginning, in more of a transverse direction. By this means a sort of posterior region is marked, which toward the posterior a sharp-angular boundary is present; however in front, a sharper boundary is absent [probably he is speaking of the cardiac region]. Inside this region hints of raised points or swellings are noticeable on the outside of the shell, which is more recognizable on the steinkern of *Prosopon rostratum* on a similar part of of the shell.

The posterior main part [area of carapace posterior to branchiocardiac groove] is without particular regions.

The thin white shell expands the entire cephalothorax. Its surface possesses a completely rough appearance, by means of densely arranged protuberances, which bear a heap in the middle. On the posterior main part they are most sharply distinct, litt. b. c. [this abbreviation may mean “for example,” G. Schweigert, pers. commun.] in its increasing size; in the front they are represented by weak depressions thereon, which appear toward the lateral side with rising-fanned-out border, which gradually increases up to the development of little pustules.

In the vicinity of this cephalothorax was marked a section of leg; it is 0.008 long and 0.002 wide.

(Translated from the original German [von Meyer, 1860], additions added in square brackets): After I established this species based upon a small incomplete cephalothorax from Aalen, I confirmed it by 17 examples from the Örlingen Valley [locality near Ulm in S Germany]. Thereby it was determined that the front-part on the complete cephalothorax [portion of carapace anterior to cervical groove] was not enclosed with a narrow, smooth side border and the spine consists of a short spiny corner corresponding to the exterior orbital angle. The small cephalothorax is 0.005 in length and .0045 in width, the widest part lying in the front-part and the width at the posterior end [of the carapace] is scarcely half as much. The largest examples attain 0.0135 length and 0.0115 width, and the largest width falls in the front-part, and posterior-wards it is less notably reduced [in width]. In front the cephalothorax is rounded and blunt-edged, and it is in the middle weakly incised and outside provided with the mentioned angle. The front-part measures half the length of the cephalothorax in the rear. Of the gastric region, only the front end is sharply distinct and not extended up to the front end of the cephalothorax and in whose vicinity the hepatic region forms a small mound on both sides [probably referring to the epigastric regions]. A pair of pores

lie in the anterior transverse [cervical] groove. The posterior transverse [branchiocardiac] groove is less strongly marked. The genital region forms in the rear a narrow, weakly expressed transverse band. The similarly weakly developed cardiac region is pentagonal, posteriorly somewhat pointed, and of almost equal length and width. In the steinkern this region has three knobs that are in a triangle form. The mound which is directed to both sides obliquely toward the cardiac region is not separated outwardly from the genital region. The posterior part itself does not reach half the length of the cephalothorax and is somewhat vaulted posteriorly. The posterior end is on the entire width weakly concave and rimmed by a narrow furrow. The shell is pustulose, but not densely and not with any strong tubercles. In the cardiac and branchial regions, where the tubercles appear organized in irregular short transverse rows, they are somewhat more densely placed.

Occurrence: Original material collected near the city of Aalen in Würtemburg, now part of the state of Baden-Württemberg, near Stuttgart. Additional material described by von Meyer (1860) was collected from the Örlinger Tal, a valley near Örlingen, about 1 km north of Ulm, in southern Germany (Swabia), where a massive limestone of upper Jurassic age (late Kimmeridgian) is exposed (G. Schweigert, pers. commun.).

Discussion: The original descriptions and illustrations of *Pithonoton marginatum* are the basis upon which our generic description of *Pithonoton* is framed. All other species that have been referred to the genus must be evaluated in terms of the original description of *Pithonoton* and its originally referred species in order to which species conform to the genus in its originally intended sense.

Pithonoton* sp. *sensu lato

(Fig. 3.1)

Description of material: Carapace small; outline apparently quadrate but poorly preserved anteriorly and posteriorly; moderately vaulted transversely, less so longitudinally; highest in posterior part of mesogastric region. Regions poorly defined. Cervical groove well defined; branchiocardiac groove equally strong laterally, not defined across axis.

Front not preserved. Orbital region poorly preserved, moderately long, directed anterolaterally, projection of orbital margins appears to converge toward long axis at 50 degree angle. Fronto-orbital width about equal to maximum width. Lateral margins parallel longitudinal axis, with shallow reentrants at extremity of cervical groove and branchiocardiac groove. Remainder of margins not preserved.

Mesogastric region obscure anteriorly and well defined posteriorly; wide, about 58 percent maximum width; defined by concave axial element of cervical groove posteriorly and by deep lateral grooves along posterolateral margin. Cardiac region subtly expressed as a transversely elongate parallelogram bearing two tiny nodes adjacent to midline. Other regions obscure.

Cervical groove with short, straight, lateral elements, projections of which intercept longitudinal axis at about 86 degree angle, and broad, uniformly concave forward axial region defining posterior margin of mesogastric region. Branchiocardiac groove well defined laterally, concave forward, terminating at extremities of cardiac region.

Ventral surface, abdomen, and appendages not preserved.

Measurements: Measurements, in mm, taken on the sole specimen of *Pithonoton* sp. *sensu lato*, LPBIIIart-041, are as follows. Maximum carapace length = 4.5, maximum carapace width = 4.3, maximum mesogastric region width = 2.5.

Material examined: LPBIIIart-041.

Occurrence: The sole specimen was collected from WP126.

Discussion: The specimen referred to *Pithonoton* sp. *sensu lato* is clearly different from all of the other specimens collected from the Romanian localities discussed herein. The specimen cannot be referred to *Goniodromites* due to its lack of lateral spines and post-cervical groove and its ovate cardiac region. It is easily differentiated from *Cycloprosopon* based upon its extremely deep branchiocardiac groove that is continuous across the dorsal carapace and well-defined cardiac region, in addition to its elongate shape. However, it is not referrable to *Pithonoton* in the strict sense either. The small, ovate cardiac region of this specimen is unlike that seen in *Pithonoton sensu stricto*, and in addition, its extremely wide posterior portion of the mesogastric region is unlike that seen in *Pithonoton sensu lato*. The specimen bears some similarities to species that have been historically referred to *Pithonoton*, such as *P. inaequilatum*, which has very deep cervical and branchiocardiac grooves such as the specimen under consideration. The specimen also bears some similarities to *Eodromites grandis* (von Meyer, 1860), also in the deep nature of the two major carapace grooves. However, the specimen here referred to *Pithonoton* sp. sensu lato is incomplete, lacking the orbits and rostrum as well as the posterior portion of the carapace (Fig. 3.1). As discussed above, *Pithonoton* currently embraces a broad morphological range that is probably untenable; when these problems are resolved, it is likely that the generic placement for *Pithonoton* sp. *sensu lato* herein illustrated will also be resolved. For now, we simply refer it to *Pithonoton* until comparative material is examined.

Genus *Goniodromites* Reuss, 1859

Iberihomola Van Straelen, 1940, p. 3, pl. I, fig. 5.

Type species: Goniodromites bidentatum Reuss, 1859.

Other species: *G. bourgeati* Van Straelen, 1925; *G. dentatum* Lőrenthey in Lőrenthey and Beurlen, 1929; *G. etalloni* (Gemmellaro, 1870), as *Prosopon*; *G. gibbosum* Etallon, 1857; *G. globosum* (Remeš, 1895, *non visus*), as *Prosopon*; *G. incisum* Van Straelen, 1925; *G. laevis* (Van Straelen, 1940), as *Iberihomola*; *G. polyodon* Reuss, 1859; *G. revili* Van Straelen, 1925; *G. scarabaeus* Wright and Wright, 1950; *G. serratus* Beurlen, 1929; *Goniodromites* sp. Forms A–C described herein. List modified after Glaessner (1929; 1933).

Diagnosis: Carapace somewhat longer than wide, as long as wide, or wider than long, maximum width ranging from 85 to 105 percent maximum length, narrowing anteriorly and posteriorly, reaching maximum width at position of intersection of cervical groove with lateral margin or at outer-orbital spine, about 30 percent the distance posteriorly on carapace. Front bilobed, frontal margins continuous with orbital margin, orbital margin can be serrate, orbital margin at about 45–50 angle to axis, outer orbital angle a well-developed spine; lateral margin with spines; dorsal carapace ornamented with tubercles anteriorly and scabrous rows of tubercles or small spines posteriorly. Cervical groove strongly developed, continuous across axis, lateral segment at 80–85 degree angle to axis. Branchiocardiac groove strongly developed laterally, less-strongly developed axially, continuous across axis, lateral segments merging posterior to cardiac region and continuing to intersect with posterior margin. Epigastric regions spherical, small; mesogastric region best defined posteriorly, anterior process often only developed near epigastric regions; cardiac region inflated; epibranchial region defined by cervical and branchiocardiac grooves.

Discussion: The generic diagnosis is based upon the original description of the type species, *Goniodromites bidentatum*, given below in translation, and the other species that Reuss (1859) originally referred to it, *G. polyodon*. The location of the types of these two species is unknown, so the concept of the genus must be based upon the original descriptions and illustrations. The descriptions of the two most commonly encountered species of the genus, *G. bidentatus* and *G. serratus*, are provided below in translation.

Table 4. Species herein referred to *Goniodromites*, arranged from youngest to oldest. Unless otherwise marked, information from Glaessner (1929).

Taxon	Age	Occurrence
G. laevis	Cenomanian	Spain (Van Straelen, 1940)
G. scarabaeus	Albian (Wright and Wright, 1950)	England (Wright and Wright, 1950)
G. bidentatum	Tithonian (Upper Jurassic)	eastern Czech Republic; ?central Romania (Patrulius, 1966); ?France (Müller *et al.*, 2000)
G. dentatum	Tithonian	Hungary
G. etalloni	Tithonian	Sicily; ?central Romania (Patrulius, 1966)
G. globosum	Tithonian	eastern Czech Republic
G. polyodon	Tithonian	Czech Republic
G. revili	Tithonian	France
G. serratum	Oxfordian, ?latest Kimmeridgian–early Tithonian (Garassino *et al.*, 2005)	Belgium, ?Poland, ?Germany (Garassino *et al.*, 2005)
G. bourgeati	Oxfordian	France
G. gibbosum	Oxfordian	France
Goniodromites sp. Forms A–C	Oxfordian	Romania
G. incisus	upper Bajocian	France

The generic status of the referred species besides the type has not been verified by examination of type material. The three species described by Van Straelen (1925) were originally referred to *Goniodromites*. He considered *Goniodromites* as a distinct genus and provided a list of diagnostic characters (Van Straelen, 1925, p. 349), some of which are included in our generic diagnosis. The description of *G. scarabaeus* corresponds well to that of the type species; however, its types and those of the other species must be examined to verify their placement. In addition, specimens collected from various localities in Europe have been referred to *G. bidentatum* and *G. etalloni* (Patrulius, 1966; Müller *et al.*, 2000), all of which would extend the range of the species as originally described. Those identifications must be confirmed through examination of referred material in order to confirm those range extensions.

Wright and Collins (1972) suggested that *Iberihomola* Van Straelen,1940, was probably a synonym of *Pithonoton*. Examination of specimens (MSB 12441, 9023) collected from the same region, Alsasua in Navarre, as the type material of the type and sole species, *Iberihomola laevis* Van Straelen, 1940, indicates that the genus is in fact synonymous with *Goniodromites*. Specimens referred to *I. laevis* are about as long as wide or wider than long and have a bifid front and long orbits; well-defined cervical and branchiocardiac grooves; a mesogastric region well-defined posteriorly and anteriorly; spherical epigastric regions; scabrous ornamentation posteriorly; and a well-defined outer-orbital spine. In addition, one of the specimens examined (MSB 12441) appears to have small granules on the orbital margin which could be broken bases of spines. All of these features are diagnostic for *Goniodromites*; thus, we synonymize *Iberihomola* with it.

The oldest known species referred to *Goniodromites* to date is *G. incisum* from the Bajocian of France (Table 4). The genus was quite speciose in the Tithonian, and extended at least into the Cenomanian of Spain.

Goniodromites bidentatus Reuss, 1859

Description (translated from the original German [Reuss, 1859], additions added in square brackets):The outline of the carapace is 0.54 [unit is unknown] long and 0.56 wide, [maximum carapace width/maximum carapace length = 1.04], hexagonal, and the greatest width lies at the end of the front portion [part of carapace anterior to cervical groove]. The front is 0.2 inches long and is inflexed in the center by a deep frontal sulcus. The anterolateral margin is short, scarcely 0.3 inches long, weakly curved, and very finely sawtoothed. Only the hindmost part extends nearly directly from the front towards the posterior and bears two relatively large, acute spines, the first of which is especially strong. The length of the posterolateral margin measures 0.3 inches and is almost straight with the exception of the weak inflection from the second transverse groove [branchiocardiac groove]. The somewhat concave terminal posterior margin is 0.21 inches long and exhibits with a small, narrow rim.

The relation between the three divisions in which the upper surface of the carapace is dissected by the two transverse furrows is different than in the following species [*G. polyodon*]. The first [portion anterior to cervical groove] is 0.3 inches long in the middle; the middle section measures 0.12 inches laterally, the posterior section however is 0.23 inches in length. The first projects forward in the center in only a weak regular bow proceding toward the front [frontal region]. The middle field [mesogastric region] is deltoidal as that in *Pithonoton*, similarly in front with a long protracted rostrum, but moderately vaulted in the rear part. Nevertheless, the anterior part of the beak-shaped process [anterior process on mesogastric region] is circumscribed most obviously by means of a narrow groove, and in front if it [the beak shaped process], the median frontal sulcus proceeds up to the frontal edge. The pronounced protuberances on both sides of this groove [epigastric regions] are vaguely expressed. The remaining part of the anterior part of the carapace exhibits a weak, uniform vault.

The middle portion of the carapace [between the cervical and branchiocardiac grooves] is elongate along the median line in a nearly equilateral triangular lobe [cardiac region] which extends deeply into the posterior portion [of the carapace], which in front is flat arched and bordered on the sides by a narrow but distinct furrow but on the front however only by a weak shallow groove. The steinkern exhibits three granules placed upon the previously mentioned triangle. The side regions exhibit no additional arrangement of parts thereon.

The rear part [part of carapace posterior to branchiocardiac groove] terminates by means of a distinct medial longitudinal groove dividing it into two moderate and equal shaped, vaulted halves.

The entire upper surface of the carapace is covered with fine roughness. On the front [portion of the carapace] they appear as flattened prominences with the points directed forward; on the middle part [of the carapace] they are expanded, squamose elevations finely crenate on the front margins. On the rear part [of the carapace] they are densely arranged and strongly forward directed. They are placed in irregular transverse rows standing as flattly pressed prominences, which if enlarged, bear 1, 2, or 3 distinctly recognizable holes which are probably broken fragments of fine spines. Because of these spines it appears that the front margin was crenate.

Occurrence: The specimen described by Reuss (1859, p. 73) was collected from the "yellow limestone of the Upper Jurassic of Semmelberg in Ernstbrunn."

Discussion: The original descriptions and illustrations of *Goniodromites bidentatus* are the basis upon which our generic description of *Goniodromites* is framed. All other species that have been referred to the genus must be evaluated in terms of the original description of *Goniodromites* and its originally referred species in order to determine which species conform to the genus in its originally intended sense.

Goniodromites serratus Beurlen, 1929

Description (translated from the original German [Beurlen, 1929], additions added in square brackets): Outline. Rounded pentagonal; largest width in anterior third. Less long than wide.

Rostrum broad, bilobed, with a rounded incision in the middle which continues on in a wide, flattened, median groove up to the front end of the mesogastric region. Orbital margin long, weakly sinuous; in specimens with preserved shell finely serrate, but smooth on the steinkern. In the outer half the orbital margin is rimmed, which disappears toward the rostrum. The orbital groove itself is wide and corresponds in its length to the orbital margin length. Toward the under side a suborbital margin is defined by means of a fully developed sharp edge like the superorbital margin.

Lateral margins rather straight, converging toward the posterior. Where the cervical and branchiocardiac grooves meet the lateral margins, they are weakly sinuous. In front of the cervical groove are found two strong lateral spines, they are larger and stronger in the examples with shell than on the steinkern. Between the cervical and branchiocardiac grooves the lateral margin is weakly sharpened and with four pointed spines, which are somewhat longer in the steinkern. The sharpness of the lateral margins is remarkably weaker, on the other hand, in the steinkern. Behind the branchiocardiac groove the protuberance row of the lateral margins extends toward the upper side: it is followed by two to three sharp protuberances, which are in a row and directed toward the inner posterior and in the steinkern are somewhat more distinct than in the upper surface of the shell. The lateral margin is widely rounded behind the branchiocardiac groove. With a blunt rounded corner the lateral margin reaches the short posterior margin which is sinuous centrally.

Upper surface: The upper surface is regular in its length and uniform and weakly vaulted both in longitudinal and in the transverse direction. Only toward the anterior end of the cephalothorax the curvature is stronger, because the rostral part is strongly downturned.

Arrangement of parts of the upper surface: The cervical groove is centrally weakly bowed toward the posterior and is equally strong in the steinkern, as well as in the shell. In the middle of the latter is a pair of large pores, those of the steinkern either are much weaker than those on the shell or perhaps are lacking and correspond to or are replaced at their positions by small protuberances. The branchiocardiac groove is strong and wide and approximately parallel to the cervical groove from the lateral margin to the cardiac region, on the shell and the steinkern. At the cardiac region these lateral segments of the branchiocardiac groove end in a wide, flat, roundish depression from which two branches extend, one toward the posterior and one toward the anterior. The posterior branch, the true continuation of the branchiocardiac groove, is very weak and delimits the posterior margin of the cardiac region. Just in front of the posterior margin of the cardiac region the branches from both sides unite into a sharp corner; which at the point of junction forms a roundish, flat, depression. A flat, wide, median groove extends [from the sharp posterior corner of the cardiac region] to the posterior margin [of the carapace], in order that the branchial region is separated into halves. The anterior branch [of the branchiocardiac groove] is likewise only weak, obliquely directed toward the front and ending at the post-cervical groove. The post-cervical groove does not extend to the lateral margins and is interrupted in the middle, so that it is formed by two short, separated, transverse grooves. These are deep and narrow both on the shell and on the steinkern: they are the deepest grooves of the whole carapace. These various grooves define a pentagonal, posteriorly sharp-ending cardiac region, which is weakly vaulted, on the steinkern bearing 3 sharp protuberances, which on the shell correspond to three flat, rounded, weak elevations.

In front of the cervical groove lies a bottle-shaped mesogastric region which is only bordered weakly and indistinctly by two weak grooves. In the hindmost part of the region there is a weak short median furrow. The anterior median groove extends from the rostral margin and divides into two grooves surrounding the mesogastric region. Two oval, rough fields immediately in front of the cervical groove are moderately distinct on the steinkern, vanishing however, in the shell almost completely. The undivided hepatic region extends with two flattened, rounded protuberances into the rostral lobes [these are the epigastric regions].

Shell sculpture: The shell is entirely ornamented with fine, round tubercles, those in front of the cervical and branchiocardiac groove are dense and irregularly distributed. From the cardiac and the posterior branchial region are tubercles in transverse, elongate orientation and arranged in irregular, transverse, wavy lines.

Occurrence: The original material was collected from the Korallenkalk (coral chalk), Côtes Lorraines, southern Belgium, apparently of Oxfordian age (Beurlen, 1928, p. 129).

Discussion: Numerous specimens have been referred to *Goniodromites serratus* in recent years, many from central and eastern Europe, quite distant from the type locality for the species. Collins and Wierzbowski (1985) considered *G. serratus* to be a distinct species and noted that there appeared to be variation in the maximum carapace length to maximum carapace width ratios among members of the species. They referred ninety-six specimens from the Oxfordian of Poland to the species, illustrating four specimens (Collins and Wierzbowski, 1985, pl. 3, figs. 2–4, pl. 4, fig. 1), which may belong to *G. serratus* based upon their possession of a weak longitudinal groove in the posterior portion of the mesogastric region and a discontinuous post-cervical groove, both characteristic of the species. It is difficult to determine if the illustrated specimens of Collins and Wierzbowski (1985) possess anterolateral spines as reported for *G. serratus*, but their absence may be due to poor preservation. Thus, these specimens are best referred to *G. serratus* until type material and the Polish specimens can be examined and compared.

The specimen referred to *Goniodromites serratus* by Müller *et al*. (2000, fig. 18C) does appear to possess the anterolateral spines typical of the species, although it lacks a well-expressed post-cervical groove and a longitudinal groove in the posterior portion of the mesogastric region. Thus, the specimen should be examined and compared to type material to confirm its placement within the species.

***Goniodromites* sp. Form A**

(Fig. 3.2)

Description: Carapace small; pentagonal; maximum width 86–92 percent maximum carapace length; maximum width measured at outer orbital node, about 38 percent maximum length from front; strongly vaulted longitudinally, more so in anterior; moderately vaulted transversely, highest point on carapace at center of mesogastric region; regions moderately well developed; cervical groove well defined, deeply impressed; branchiocardiac groove equally developed as cervical groove laterally, less well developed axially, crosses midline at posterior margin of cardiac region.

Front narrow, about 26 percent maximum width, downturned, sulcate, tapering; may be bifid. Orbits long; orbital margin continuous with frontal margin, weakly concave, becoming more strongly concave at lateral corner of orbit, which is defined by blunt outer orbital node; projection of orbital margin intercepts longitudinal axis at approximately 50 degree angle. Lateral margins with pronounced indentations marking extremities of cervical and branchiocardiac grooves, both of which extend onto lateral flanks; two small, blunt nodes on margin between grooves; margin nearly straight from branchiocardiac groove to sharply rounded posterolateral corner. Lateral flanks distinct, vertical or slightly inturned. Posterior margin concave, rimmed, about half maximum width.

Epigastric regions distinctly elevated, circular; diameter about 14 percent maximum width. Protogastric and hepatic regions not differentiated. Mesogastric region well defined, pyriform; anterior element arises at level of maximum width of epigastric nodes, bounded by distinct depressions that merge anteriorly with rostral sulcus; anterior element more or less lanceolate in outline, narrowing slightly before broadening into triangular posterior element whose maximum width is about 40–42 percent maximum carapace width. Metagastric and urogastric regions lie between cervical and branchiocardiac grooves; slightly wider than mesogastric region, concave forward; metagastric region about twice as long as urogastric region and less well defined laterally than urogastric region; urogastric region constricted axially. Post-cervical groove moderately well-defined. Cardiac region an equilateral triangle, broadest anteriorly, weakly inflated, bounded laterally by distinct grooves. Intestinal region long, marked by shallow, distinct groove formed by confluence of branchiocardiac grooves. Epibranchial region quadrate, bounded by cervical and branchiocardiac grooves. Remainder of branchial area weakly

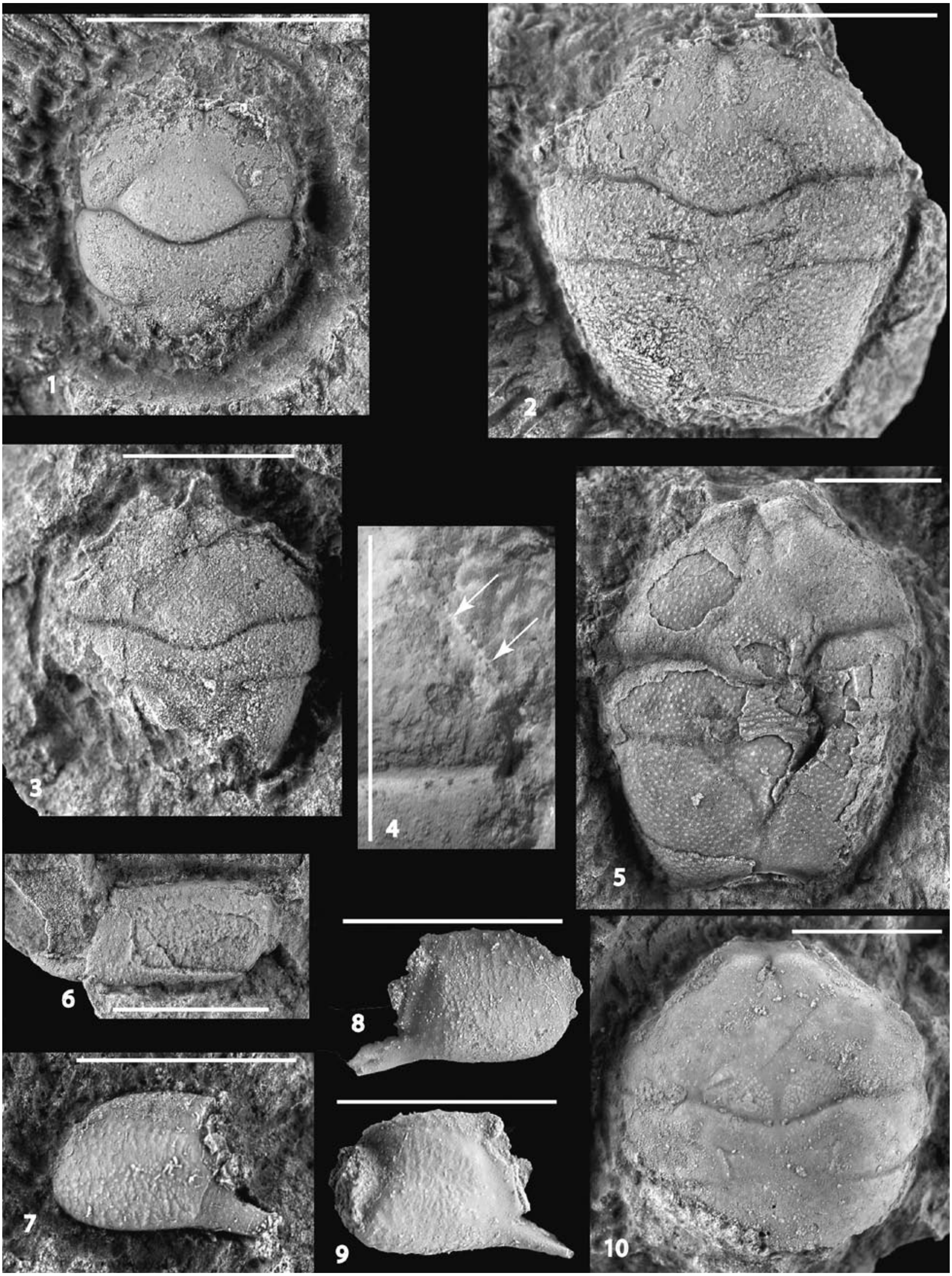

Fig. 3. 1, *Pithonoton* sp. *sensu lato*, LPBIIIart-041. 2, *Goniodromites* sp. Form A, LPBIIIart-042. 3, *Goniodromites* sp. Form C, LPBIIIart-032. 4, Closeup of the orbital margin of *Goniodromites* sp. Form C, LPBIIIart-033, showing serrated margin between arrows. 5, *Goniodromites* sp. Form B, LPBIIIart-047. 6, Indeterminate chela 2, LPBIIIart-050, exposing outer surface of left propodus. 7, Indeterminate chela 1, LPBIIIart-049, exposing outer surface of right propodus. 8, 9, Indeterminate chela 1, LPBIIIart-048, exposing outer and inner surfaces, respectively, of left chela. 10, *Cycloprosopon dobrogea* n. sp., holotype, LPBIIIart-040. Scale bars for all figures except 6–9 = 1 cm. Scale bars for figures 6–9 = 0.5 cm.

inflated.

Cervical groove concave forward; lateral elements straight, projection of them intercepts longitudinal axis at 88 degree angle; axial segment more strongly concave, defining posterior margin of mesobranchial region. Branchiocardiac groove weakly concave forward laterally and approximately parallel to lateral elements of cervical groove; branchiocardiac groove curves posteriorly as straight elements defining lateral margins of cardiac region and merging at apex of cardiac region to form axial depression in intestinal region.

Carapace surface very finely scabrous in branchial regions, becoming very finely pustulose anteriorly.

Ventral surface, abdomen and appendages not preserved.

Measurements: Measurements, in mm, taken on specimens of *Goniodromites* species Form A are given in Table 5.

Table 5. Measurements (in mm) taken on specimens referred to *Goniodromites* sp. Form A. L = maximum carapace length, W = maximum carapace width, FW = frontal width, FOW = fronto-orbital width, PW = posterior width, MgW = maximum mesogastric width.

Specimen	L	W	FW	FOW	PW	MgW
LPBIIIart-044	6.5	5.7	—	ca. 5.7	3.1	2.4
LPBIIIart-042	10.2	9.4	—	—	4.3	3.8
LPBIIIart-045	6.3	5.8	1.5	5.5	3.1	2.3
LPBIIIart-043	4.4	3.8	1.0	3.8	ca. 1.7	ca. 1.6

Material examined: LPBIIIart-042–LPBIIIart-046.

Occurrence: LPBIIIart-042 was collected from WP 126, and two specimens each from WP 125 (LPBIIIart-045 and 046) and WP 127 (LPBIIIart-043 and 044).

Discussion: Several specimens were collected from the three major facies of the sponge–algal reef environment that are referrable to *Goniodromites*. The specimens are separable into three distinct forms, but based upon reported variation within populations of *Goniodromites* (Collins and Wierzbowski, 1985; Müller *et al*., 2000) as well as the fact that type material for many species of *Goniodromites* either has been lost or not yet examined by us, we are hesitant to create three separate species for this material.

Form A is by far the best preserved and represented of the three forms. The dorsal carapace of several of the specimens of Form A are reasonably complete and show clearly defined margins, groove patterns, and ornamentation. Form A differs from Form B, to be described below, in the width of the mesogastric region compared to the maximum width of the carapace which is higher in Form A, averaging about 41 percent; whereas, in Form B it is about 35 percent. Form A is ornamented by two nodes on the lateral margins between the intersection of the cervical and branchiocardiac grooves but Form B lacks these nodes. Forms A and B differ from Form C to be described below in lacking tiny spines on the orbital margin, which Form C possesses. The mesobranchial region is wider with respect to the maximum width in Form C than in either Form A or B, and the lateral segment of the cervical groove is at a lower angle to the axis, about 75 degrees, in Form C than in Form A or B, in which it is about 88 degrees and 82 degrees respectively. The branchiocardiac groove is very weak axially in Form C and weaker than in either of the other two forms.

Thus, there are very clear points of distinction among the three forms herein referred to *Goniodromites*. As discussed by both Collins and Wierzbowski (1985) and Müller *et al.* (2000), *Goniodromites* can vary considerably in its ratio of maximum carapace width to maximum carapace length. In addition, our perusal of the literature suggests that the number of lateral spines can be variable, even within the same specimen (Wright and Wright, 1950) (Table 6). Because specimens of *Goniodromites* are so often lacking cuticle, it is also possible that cuticle loss could lead to the loss of the very delicate spines on the orbital margins and even small spines on the lateral margins; thus, it is possible that many species currently described as lacking orbital spines or serrations may in fact have possessed them. Cuticle loss and the differential preservation between cuticle and steinkerns also leads to different interpretations of the depth of the carapace grooves; for example, Beurlen (1929) described the post-cervical grooves as being the deepest grooves on the carapace. Based upon all of our observations of the specimens of *Goniodromites*, this seems highly

Table 6. Species referred to *Goniodromites* and differentiating characters. W/L = maximum carapace width/maximum carapace length; SA = number of lateral spines or nodes anterior to intersection of cervical groove with lateral margin including outer orbital spine; SB = number of lateral spines or nodes between intersection of cervical and branchiocardiac grooves with lateral margin; PC = development of post-cervical groove; PMG = posterior mesogastric longitudinal groove; MW = mesogastric width/maximum carapace width; SOM = serrate orbital margin. * measured from line drawing; ** estimated from very poor illustration.

Species	W/L	SA	SB	PC	PMG	MW	SOM
G. bidentatus (type)	1.04	2	0	weak	absent	0.37	yes
G. serratus	> 1.00	2	4	deep	present	0.43*	yes
Goniodromites sp. Form A	0.86-0.92	1	2	moderate	absent	0.40–0.42	no
Goniodromites sp. Form B	0.83	1	0	weak	absent	0.35	no
Goniodromites sp. Form C	∼ 1.00	0	0	moderate	absent	0.46	yes
G. dentatus	-	2	2	weak	absent	0.40	no
*G. gibbosum***	1.00	1	0	-	absent	0.50	no
G. polyodon	0.98	2	0	moderate	present	0.43	no
G. etalloni	1.07	1	0	weak	absent	0.40	no
G. laevis	∼ 1.00	1–3	1–3	weak	absent	∼ 0.50	?
G. scarabaeus	0.90	2–3	2–3	moderate	present	0.41	no

unlikely, but until type material is examined, we must accept the original description. Thus, at this time we feel that it is most prudent to assign these specimens of *Goniodromites* as simply forms until they can be compared to material referred to other species of the genus in order to determine the true range of variation within species of *Goniodromites*.

The three forms do not appear to be referrable to previously named species of *Goniodromites*. Form A differs from *Goniodromites serratus* in lacking four lateral spines between the intersection of the cervical and branchiocardiac grooves on the lateral margins of the dorsal carapace; the longitudinal groove in the posterior portion of the mesogastric region; and the well-defined post-cervical groove, all of which *G. serratus* possesses. *Goniodromites bidentatus* possesses two large spines anterior to the intersection of the cervical groove with the lateral margin, which Form A lacks and instead possesses two blunt nodes between the intersection of the cervical and branchiocardiac grooves with the lateral margin. *Goniodromites dentatus* possesses two large spines anterior to the intersection of the cervical groove with the lateral margin and two large spines posterior to that intersection; Form A only possesses blunt nodes posterior to the intersection of the cervical groove with the lateral margin. *Goniodromites polyodon* possesses a forward directed outer-orbital spine and a laterally directed lateral spine posterior to the outer-orbital spine in addition to a longitudinal keel on the mesogastric region, all of which Form A lacks. *Goniodromites etalloni* possesses a marked forward directed outer-orbital spine, not seen in Form A; in addition, the cervical groove of *G. etalloni* intersects the lateral margins of the carapace much further anteriorly than in Form A.

***Goniodromites* sp. Form B**

(Fig. 3.5)

Diagnosis: Carapace longer than wide, maximum width about 83 percent maximum length, widest just posterior to the position at which the cervical groove intersects the lateral margins; mesogastric width about 35 percent maximum carpace width; lateral margins without spines or nodes.

Description: Carapace large, elongate ovoid to pentagonal; maximum width 83 percent maximum length; maximum width measured just posterior to cervical groove extremities, about 37 percent the distance posteriorly; weakly vaulted transversely and longitudinally; highest point on carapace in mesogastric region; axial regions well defined; lateral regions obscure; cervical groove well defined, deeply impressed; branchiocardiac groove less defined than cervical groove, becoming even less well defined as it crosses midline posterior to cardiac region.

Front about 27 percent maximum width, projected slightly in advance of orbits, weakly convex forward, axially sulcate. Orbits moderately long, directed anterolaterally, weakly concave; projection of orbits intercepts longitudinal axis at 48 degree angle; outer orbital corner defined by inflection of margin and tiny node, inner orbital corner may also be defined by inflection and node. Lateral margin convex anterior to cervical groove re-entrant and very weakly convex posterior to cervical groove, converging on longitudinal axis at 18 degree angle. Posterolateral corner distinct, curving abruptly into concave, rimmed posterior margin.

Epigastric regions prominent, circular, about 11 percent maximum carapace width. Protogastric and hepatic regions not differentiated. Mesogastric region pyriform, defined by shallow marginal depressions laterally and axial segment of cervical groove posteriorly; narrow anterior process arises posterior to maximum diameter of epigastric region, straight sided, broadening posteriorly into triangular posterior element about 35 percent maximum width. Metagastric and urogastric regions lie between cervical and branchiocardiac grooves, as wide as mesogastric region; urogastric region half as long as metagastric region. Cardiac region triangular, broadest anteriorly, weakly inflated, bounded laterally by shallow, subtle grooves formed by confluence of branchiocardiac grooves. Epibranchial region quadrate, bounded by cervical and branchiocardiac grooves. Remainder of branchial region undifferentiated, weakly inflated.

Cervical groove concave; lateral elements straight, projection of lateral elements intercepts long axis of carapace at 83 degree angle; axial segment more strongly concave defining posterior margin of mesogastric region. Lateral elements of branchiocardiac groove parallel lateral elements of cervical groove; branchiocardiac groove curving posteriorly as subtle, straight elements defining lateral margins of cardiac groove and merging at apex of cardiac region, then widening to form shallow, circular depression in intestinal region.

Carapace surface with transverse scabrous ornamentation posterior to cervical groove and finely pustulose in anterior regions. Surface of mold of interior finely pustulose throughout.

Ventral surface, abdomen, and appendages not preserved.

Measurements: Measurements, in mm, taken on the sole specimen of *Goniodromites* sp. Form B, LPBIIIart-047, are as follows. Maximum carapace length = 17.2; maximum carapace width = 14.2; frontal width = 3.8; fronto-orbital width = 11.8; posterior width = 6.8; mesogastric width = 5.0.

Material examined: LPBIIIart-047.

Occurrence: The sole specimen was recovered from WP 127.

Discussion: *Goniodromites* sp. Form B differs from all other species herein referred to the genus in its narrow carapace; all other species are about as wide as long or slightly wider than long. *Goniodromites dentatus* and *G. serratus* possess several lateral spines, which *G.* sp. Form B lacks. Both *G. polyodon* and *G. etalloni* possess long outer-orbital spines, which *G.* sp. Form B lacks. Form B has already been differentiated from the other two forms herein described.

***Goniodromites* sp. Form C**

(Figs. 3.3, 3.4)

Diagnosis: Carapace slightly wider than long, maximum width defined at extremities of cervical groove; orbital margin with tiny spines; mesogastric width about 46 percent maximum width; lateral segments of cervical groove intercept longitudinal axis at 75 degree angle; branchiocardiac groove moderately defined laterally, very weakly defined across axial regions

Description: Small size for genus; elongate hexagonal in outline; slightly longer than wide; maximum width defined at extremities of cervical groove situated 27 percent of total length from front of carapace; moderately vaulted transversely and longitudinally; highest at posterior part of mesogastric region, just posterior to midlength. Regions poorly defined. Cervical groove well developed; branchiocardiac groove moderately defined laterally, weakly defined across axial regions.

Front poorly preserved; approximately 20 percent maximum width; downturned, axially sulcate, tapering to narrow, rounded tip. Orbits long, straight, directed anterolaterally, projection of orbital margin intercepts longitudinal axis at 48 degree angle. Fronto-orbital width approximately 93 percent maximum width. Orbital margin rimmed by very tiny spines. Lateral margin very slightly convex from outer orbital corner to posterior corner except where crossed by cervical and branchiocardiac grooves; converging slightly posteriorly. Posterolateral corners smoothly rounded. Posterior margin broad, about 55 percent maximum width, weakly convex forward.

Epigastric regions small, subtly expressed as low domes. Mesogastric region pyriform with narrow, weakly expressed anterior process, slightly elevated axially, and broadening into more distinct, triangular area about 46 percent maximum width. Weak post-cervical groove separating metagastric and urogastric regions. Other regions indistinct.

Cervical groove complete, well developed, concave forward; lateral segments nearly straight, projection of lateral segments intercept longitudinal axis at 75 degree angle then becoming more strongly concave where it defines posterior margin of mesogastric region. Branchiocardiac groove less well developed, approximately parallel lateral segments of cervical groove, becoming obscure and weak axially.

Ventral surface, abdomen, and appendages not preserved.

Measurements: Measurements, in mm, are given in Table 7.

Table 7. Measurements (in mm) taken on specimens of *Goniodromites* sp. Form C. L = carapace length, W = maximum carapace width, FW = frontal width, FOW = fronto-orbital width, PW = posterior width, MgW = maximum mesogastric width.

	L	W	FW	FOW	PW	MgW
LPBIIIart-030	—	9.0	—	8.0	—	—
LPBIIIart-032	ca. 6.5	ca. 5.6	ca. 1.2	ca. 5.2	—	—
LPBIIIart-031	ca. 7.4	7.2	—	—	4.0	—
LPBIIIart-028	10.6	8.2	—	—	ca.5.2	—
LPBIIIart-033	8.5	9.4	—	—	—	3.2

Material examined: LPBIIIart-028–LPBIIIart-033.

Occurrence: Three specimens (LPBIIIart-028–LPBIIIart-030) were collected from WP 126, and three specimens (LPBIIIart-031–LPBIIIart-033) were collected from WP 127.

Discussion: *Goniodromites* sp. Form C has already been differentiated from the other two forms described here. The combination of a very weak branchiocardiac groove and well-developed orbital spines (Fig. 3.4) differentiates Form C from all other species of the genus as well. In addition, Form C exhibits no evidence of lateral spines between the intersection of the cervical and branchiocardiac grooves with the lateral margins nor any spines anterior to the intersection of the cervical groove with the lateral margin; lateral spines are seen in *G. polyodon*, *G. etalloni*, *G. bidentatus*, *G. serratus*, and *G. dentatus*.

Genus *Cycloprosopon* Lőrenthey *in* Lőrenthey and Beurlen, 1929

Type species: *Cycloprosopon typicum* Lőrenthey *in* Lőrenthey and Beurlen, 1929, by original designation.

Included species: *Cycloprosopon complanatiforme* (Moericke, 1889), as *Prosopon*; *C. dobrogea* new species; *C. latum* (Moericke, 1889), as *Prosopon*, and *C. typicum*. Both Lőrenthey *in* Lőrenthey and Beurlen (1929) and Glaessner (1929) also included *C. reussi* (Gemmellaro, 1870), as *Prosopon*; *C. rotundum* Beurlen, 1925; and *C. tithonium* (Gemmellaro, 1870), as *Prosopon*, in the genus. The status of those three species has not yet been resolved because of the lack of detailed descriptions and illustrations for them; confirmation of their generic placement must await examination of literature and/or type material.

Diagnosis (translation from the original German in first paragraph): The small cephalothorax is generally wider than long. The sides are smooth and pass perfectly into one another, and in particular, the frontal margin is never separated from the anterolateral margin through a corner. The surface is smooth, without any larger elevations, the regions are not separated from each other, and sometimes only the cervical groove is clearly distinguishable. A rostral lobe is absent (Lőrenthey *in* Lőrenthey and Beurlen, 1929).

Dorsal carapace circular to ovate. Front bilobed, orbits merging with anterolateral margin with no inflection or spine; cervical groove well-defined laterally, usually well-defined across axis but may be weaker in axial area; branchiocardiac groove sometimes present, weaker than cervical groove; posterior margin short, concave. Carapace surface smooth or with small tubercles. Mesogastric region moderately defined anteriorly, sometimes weakly outlined posteriorly; epigastric regions weakly inflated; remainder of carapace regions not defined.

Discussion: Herein we confidently place four species within the genus, because they form a tight morphological cluster, and as noted above, the other species will need to be examined before referral can be confirmed. It is worth noting that a specimen illustrated as *Pithonoton* (*Cycloprosopon*) *reussi* by Bachmayer (1948) appears to fit the diagnosis of *Cycloprosopon* provided here, but again, the original types of *Prosopon reussi* will need to be examined to confirm placement in *Cycloprosopon*. Lőrenthey *in* Lőrenthey and Beurlen (1929) had also referred *Prosopon simplex* von Meyer, 1840, and *Pithonoton rostratum* von Meyer, 1842, to their subgenus *Cycloprosopon*. Glaessner (1929) placed *Prosopon simplex* within *Pithonoton*; type material or illustrations will have to be examined to confirm this placement. *Pithonoton rostratum* is clearly longer than wide, has a produced rostrum, defined axial regions, and a deeply incised branchiocardiac groove, eliminating it from *Cycloprosopon* (von Meyer, 1842, pl. XV, fig. 5). Patrulius (1966) considered this species to be a member of *Eodromites* Patrulius, 1959; specimens of *P. rostratum* must be examined to test this placement. For now, we concur with Glaessner's (1929) retention of *Pithonoton rostratum* in *Pithonoton*.

Lőrenthey *in* Lőrenthey and Beurlen (1929) hinted that *Pithonoton grande* von Meyer (1860) may be an "extreme form" of *Cycloprosopon*. That species is clearly longer than wide, has deeply incised cervical and branchocardiac grooves, and has a deep, concave groove connected to the branchiocardiac groove along the urogastric region not seen in *Cycloprosopon*. In addition, specimens referred to *Pithonoton grande* after von Meyer's original description and Moericke's (1889) subsequent reillustration are better preserved and have well-defined axial and epibranchial dorsal carapace regions. Patrulius (1959) erected the genus *Eodromites* to accommodate this species, with which we concur.

The confirmed species of *Cycloprosopon* are all known from Jurassic rocks of central and eastern Europe. The earliest known species of the genus is the new species, from Oxfordian rocks of eastern-most Romania. Each of the other three species, *C. complanatiforme*, *C. latum*, and *C. typicum*, is known from the Tithonian, the first two from what is now the eastern Czech Republic, and the third from what is now Romania. The latter locality lies in Transsylvania which, in 1929, was a part of Hungary.

Cycloprosopon dobrogea **new species**

(Fig. 3.10)

Diagnosis: Carapace about as wide as long, circular; mesogastric region pyriform, very subtly expressed; narrow anterior process arises at level of broadest part of epigastric regions; broadest part of mesogastric region defined as point of inflection of cervical groove about 50 percent maximum width; cervical groove well-defined; well-defined branchiocardiac groove extending across the branchial regions, terminating before reaching the axial regions.

Description: Small to moderate size for genus; nearly circular in outline, length and width approximately equal; maximum width situated 46 percent of total length from front of carapace. Moderately vaulted transversely and longitudinally; highest in posterior part of mesogastric region, posterior to midlength. Regions poorly defined. Cervical groove well-defined; branchiocardiac groove not defined across axial regions.

Front broad, approximately 25–35 percent maximum width measured just posterior to orbits; downturned, axially depressed, blunt termination; bordered by narrow, smooth rim that continues the length of orbits. Orbits long, weakly concave, directed anterolaterally; projection of orbital margin intercepts longitudinal axis at about 50 degree angle. Fronto-orbital width about 98 percent maximum width. Lateral margin smoothly convex, except with reentrants where crossed by cervical and postcervical grooves, and apparently merging with narrow, convex posterior margin.

Table 8. Measurements (in mm) taken on specimens of *Cycloprosopon dobrogea* new species. L = maximum carapace length, W = maximum carapace width, FW = frontal width, FOW = fronto-orbital width, PW = posterior width, MgW = maximum mesogastric width.

Specimen	L	W	FW	FOW	PW	MgW
LPBIIIart-034	Crushed					
LPBIIIart-038	12.0	11.6	—	11.1	ca. 5.8	4.6
LPBIIIart-035	6.0	5.8	ca. 1.3	5.7	—	2.9
LPBIIIart-037	ca. 8.3	8.0	ca. 2.0	—	—	4.2
LPBIIIart-040 (Holotype)	8.3	8.7	3.1	ca. 8.7	—	4.4

Epigastric regions distinctly inflated as circular, to slightly elongate regions, the diameter of each about 14 percent maximum width. Mesogastric region pyriform, very subtly expressed; narrow anterior process arises at level of broadest part of epigastric regions; broadest part of mesogastric region defined as point of inflection of cervical groove about 50 percent maximum width. Other regions indistinct.

Cervical groove complete, well developed, concave forward; lateral segments weakly concave forward, projection of segments intercepting longitudinal axis at about 80 degree angle then becoming more strongly concave where it defines posterior margin of mesogastric region. Branchiocardiac groove equally well developed laterally, parallel to lateral elements of cervical groove and becoming obscure and disappearing axially.

Ventral surface, abdomen, and appendages not preserved.

Measurements: Measurements, in mm, taken on specimens of *Cycloprosopon dobrogea* new species are given in Table 8.

Etymology: The trivial name is the name of the region of Romania from which the specimens were collected.

Types: Holotype, LPBIIIart-040, and six paratypes, LPBIIIart-034–LPBIIIart-039.

Occurrence: The holotype (LPBIIIart-040) was collected from WP 125, five specimens from WP 126 (LPBIIIart-035–LPBIIIart-039), and one specimen (LPBIIIart-034) from WP 127.

Discussion: *Cycloprosopon dobrogea* differs from all other species of the genus in having a well-defined branchiocardiac groove that extends across the branchial regions, terminating before reaching the axial regions. Other species of the genus either lack a branchiocardiac groove altogether or have a less deeply incised groove, as in *C. complanatiforme*.

Of the specimens referred to *Cycloprosopon dobrogea*, one specimen is crushed in a brittle fashion. All of the specimens are preserved as molds of the interior, introducing the possibility that the dorsal carapace ornamentation may in fact have been more pronounced.

Indeterminate chela sp. 1

(Figs. 3.7–3.9)

Description of material: Left propodus with hand longer than high, height 70 percent length; more strongly convex on outer than inner surface. Proximal articulation oblique to long axis of hand, intercepts long axis at 83 degree angle; length of articulation about 60 percent height of hand. Upper surface of hand convex with three tiny spines. Distal margin with small swelling at upper point of articulation with dactylus; another bulbous swelling below that; and a large triangular projection extending to lower point of articulation with dactylus. Small, pustulose swelling situated just above fixed finger. Lower surface weakly convex, smooth. Inner and outer surfaces with very fine, transverse scabrous ornamentation. Fixed finger short, straight, uniformly tapering; lower surface inclined 12 degrees downward from long axis of hand. Occlusal surface flattened, smooth axially and armed with at least two sharp distally directed spines situated along outer margin.

Right propodus similar to left but more stout, height 79 percent length.

Measurements: Measurements, in mm, on the two specimens referred are given here. LPBIIIart-048, left chela: length of manus = 3.3; height of manus = 2.3; length of fixed finger = 4.0. LPBIIIart-049, right chela: length of manus = 3.4; height of manus = 2.7; length of fixed finger = 4.2.

Material examined: LPBIIIart-048–LPBIIIart-049.

Occurence: Both specimens were collected from WP 125.

Discussion: The specimens were not found associated with dorsal carapace material. It is possible that they, as well as the chela described below, belong to members of the Prosopidae because all of the carapace material recovered in association with the chelae is referrable to the family. However, it is also possible that the chelae may be referrable to thalassinoid or paguroid groups with carapace material with poor preservation potential.

Indeterminate chela sp. 2

(Fig. 3.6)

Description of material: Propodus of left cheliped with elongate, rectangular hand, height 58 percent length. Upper and lower margins weakly convex, smooth. Proximal articulation lies at right angles to long axis of hand; proximal part of outer surface of hand inclined at about 103 degrees to long axis of hand. Distal margin of hand inclined about 109 degrees to long axis of hand. Surface of hand poorly preserved. Fixed finger short, curving upward in smooth arc; lower surface smooth, occlusal surface appears to have at least one domed denticle.

Measurements: Measurements, in mm, taken on the sole specimen referred to Indeterminate chela sp. 2, LPBIIIart-050: length of manus = 5.0; height of manus = 2.9; total length of fixed finger = 7.0.

Material examined and occurrence: LPBIIIart-050 was collected from WP 126.

Taphonomy

The decapods collected from all three facies within the sponge-algal reef complex are typically preserved as molds of the interior of the carapace. Thin, often chalky, bits of carapace material are adherent to the molds in about 40 percent of the specimens. Presence of dendrites on both mold surfaces and cuticle (Figs. 4.2, 4.3) suggest that these interfaces provided an avenue for passage of fluids which may have degraded the cuticle. When part and counterpart of specimens were collected, cuticular material was observed adhering to the counterpart in a manner similar to that described by Waugh *et al*. (2004) suggesting that separation of the part and counterpart between the exocuticle and endocuticle occurs in a manner similar to that seen in Cretaceous and Cenozoic decapods preserved within concretionary structures. The remains of the cuticle range from tiny fragments to about half of the original cuticle surface (Fig. 4.1). In the taxa exhibiting nodes, pustules, or other surface sculpture, the pattern of sculpture is evident, but muted, on the surface of the mold of the interior (Fig. 4.2). Thus, characterization of surface sculpture in moldic fossils should provide useful information about actual surficial sculpture in many cases. However, some very fine details of surface features may not be replicated on the molds. For example, the very fine serrations on the orbital margin of *Goniodromites* sp. Form C are preserved on the cuticular surface, but it is unknown whether or not the features would be expressed on the molds (Fig. 3.4). This is significant because these serrations have been taken to have taxonomic significance, and their absence on molds could affect taxonomic judgements. Microscopic examination of fractured edges of the cuticle indicates that little or no original microstructure is preserved. Examination of the literature on prosopids indicates that this pattern of preservation of moldic fossils with little remaining cuticle is typical of preservation of the group.

Only three isolated claws were collected, and these were dissociated from the carapaces so that it is not possible to relate the claws to any of the carapaces with certainty. Claws associated with prosopids are apparently rare. Quenstedt (1859, fig. 95) illustrated three claws from Jurassic rocks containing *Prosopon*, but referred to them in the text only as brachyuran claws. At about the same time Étallon (1859[III in explanation]) assigned a claw to *Pithonoton meyeri* and another claw to *P. quadratum*. Based upon the illustrations (Étallon, 1859, pl. T), the claws were separated from the carapaces so that the association is circumstantial. Von Meyer (1860) illustrated three claws which were assigned to prosopid taxa including one (1860, pl. 23, fig. 40) that he suggested might belong to *Prosopon elongatum*. Again, the association is circumstantial. Finally, Garassino *et al*. (2005) described a very poorly preserved articulated specimen from the Upper Jurassic of Bavaria which they assigned to *Pithonoton* sp. If the specimen can be confirmed as a representative of the genus, it would constitute the first member of the genus to be preserved with appendages in place.

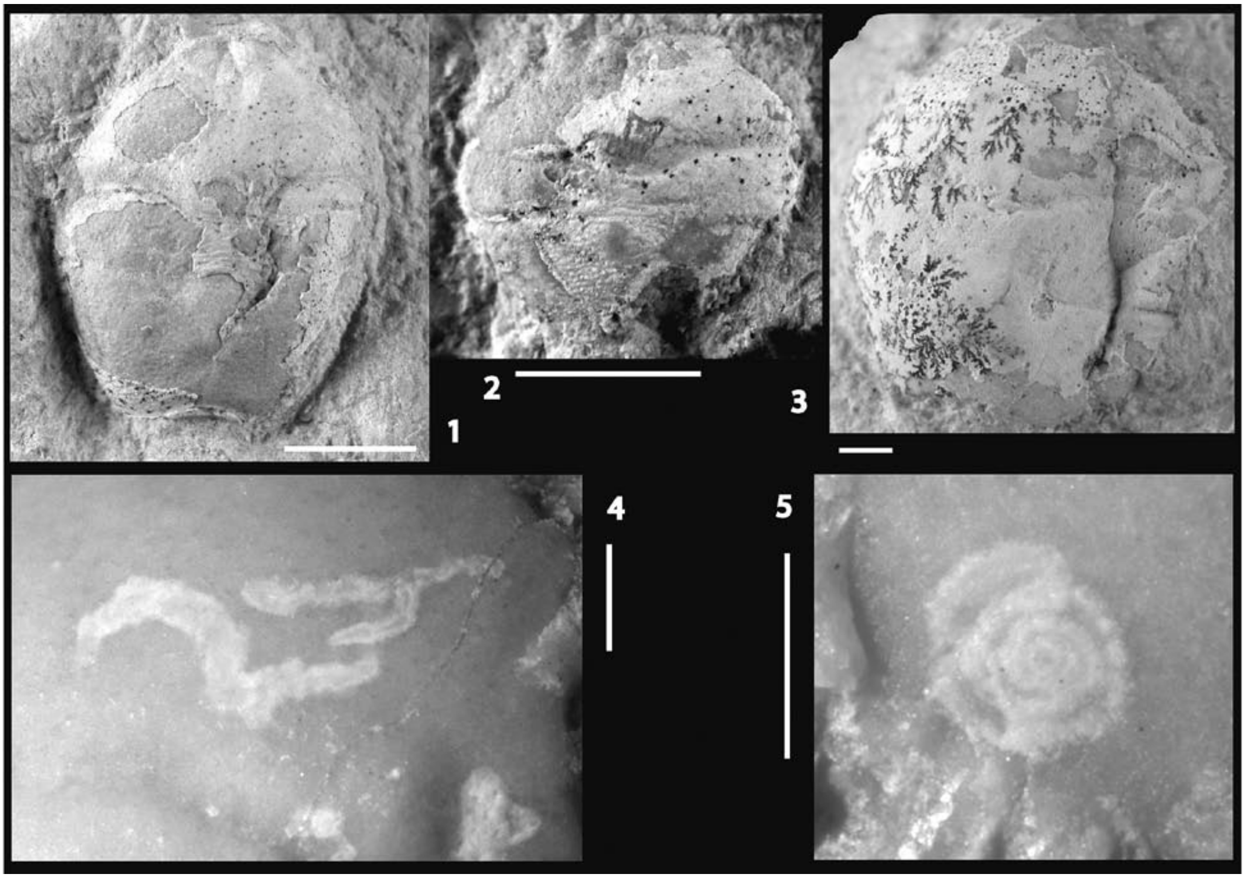

Fig. 4. 1, Unwhitened illustration of *Goniodromites* sp. Form B, LPBIIIart-047, showing brittle crushing in the right branchial region and subdued expression of surface sculpture on the moldic surface; black spots are dendrites. 2, Unwhitened illustration of *Goniodromites* sp. Form C, LPBIIIart-033, showing subdued expression of surface sculpture on the moldic surface; black spots are dendrites. 3, Unwhitened illustration of *Cycloprosopon dobrogea* n. sp., paratype, LPBIIIart-034, showing brittle crushing on the right side of the specimen; black dendritic markings are dendrites. 4, Closeup of moldic surface of *Cycloprosopon dobrogea* n. sp., paratype, LPBIIIart-038, showing presumed traces of worm browsing. 5, Closeup of moldic surface of *Cycloprosopon dobrogea* n. sp., paratype, LPBIIIart-038, showing attachment trace of a foraminiferan. Scale bars for figures 1 and 2 = 1 cm. Scale bars for figures 3–5 = 1 mm.

However, comparison of the outline of the carapace and, particularly, the morphology of the claw with extant decapods strongly suggests that the specimen is a porcellanid, comparable to *Petrolisthes* Stimpson, 1858. If that can be confirmed, it would represent the oldest record of the family Porcellanidae Haworth, 1825.

All the specimens collected from the sponge-algal bioherm are disarticulated; that is, the carapaces are preserved in the absence of sterna, abdomina, and appendages. Likewise, the claws are preserved as isolated elements. Examination of the literature on prosopids indicates that this is the general rule. No member of the Prosopidae has been preserved that is articulated, to our knowledge. This is significant because both the claws and the carapace are well calcified, based upon observation of our specimens. Furthermore, the specimens that are preserved within the reef mass were likely preserved near their living site and were entombed in a relatively protected site where articulated specimens might be anticipated. The general small size of the individuals should have further enhanced their possibilities for preservation in their entirety.

That the carapace was well calcified is further documented by the observation that one specimen of *Goniodromites* species Form B and one of *Cycloprosopon dobrogea*, both from the inter-reef talus, are crushed and the lines of breakage would only have resulted if the carapace was brittle and, therefore, well-calcified (Figs. 4.1, 4.3). Absence of fractures in the surrounding matrix supports the interpretation that the fracturing of the carapaces probably occurred upon compaction of the sediment, shortly after burial of the specimens.

The prosopids identified from the sponge–algal reef complex do not exhibit any indication of infestation by bopyrid isopods, although they have been noted previously from Oxfordian prosopids in Poland (Radwański, 1972). Bopyrids are widely known in fossil and extant decapods (see Feldmann, 2003, for summary and references) ranging from Oxfordian to the present. None has yet been described from Romania.

A single specimen of *Cycloprosopon dobrogea* new species does exhibit evidence of epibionts (Figs. 4.4, 4.5). Sinuous traces across the mold of the interior of the carapace, about 0.5 mm in width, appear to have been constructed by an organism scavenging on the under-surface of the carapace. Additionally, a single circular impression, about 0.8 mm in diameter, situated in the cardiac region on the mold of the interior of the carapace is the attachment scar of a sessile, coiled, multi-chambered foraminiferan, possibly a representative of the Ophthalmidiidae. Presence of this biotic activity on the inner surface of the carapace supports the contention that the carapace was lying free on the substratum for a sufficient time that attachment could occur.

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