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# Revision of the Prosopinae *sensu* GLAESSNER, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species

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(With 10 figures and 8 tables)

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## Summary

Re-evaluation of the Prosopinae VON MEYER, 1860 (*sensu* GLAESSNER, 1969) has resulted in placement of the included genera into two superfamilies, the Homolodromioidea ALCOCK, 1900, and Glaessneropsoidea PATRULIUS, 1959. The previously recognized Goniodromitidae BEURLEN, 1932, and Tanidromitidae SCHWEITZER & FELDMANN, 2008 [imprint 2007], are confirmed as belonging to the Homolodromioidea. New taxa recognized herein include four new families, Bucculentidae, Lecythocaridae, Longodromitidae, and Nodoprosopidae; four new genera, *Abyssopthalmus*, *Bucculentum*, *Protuberosa*, and *Verrucarcinus*; five new species, *Bucculentum bachmayeri*, *Glaessneropsis myrmekia*, *G. tribulosa*, *Lecythocaris obesa*, and *Prosopon abbreviatum*; and eight new combinations. Taxa are classified based upon a comprehensive array of characters including features of the orbits and rostrum; the nature and development of the carapace grooves; and the development of the dorsal and subdorsal carapace regions. A new term is defined, augenrest, for the concavity in the dorsal carapace or frontal margin of the carapace that lies distal to the orbit to house the eye. Recognition of two superfamilies for these taxa confirms the previous hypotheses of FELDMANN et al. (2006), SCHWEITZER et al. (2007), and SCHWEITZER & FELDMANN (2008 [imprint 2007]) that Jurassic Brachyura were much more diverse than previously recognized.

**Keywords:** Prosopinae, Brachyura, Decapoda, Revision, New Taxa, Jurassic

## Introduction

The Prosopidae VON MEYER, 1860, has conventionally been considered one of the basal families within the Dromiacea DE HAAN, 1833, and to be among the oldest and most primitive brachyuran groups. As such, they take on considerable significance in interpreting the early history and diversification of the Brachyura as a group. GLAESSNER (1969) divided the family into three subfamilies, the Prosopinae VON MEYER, 1860; Pithonotinae GLAESSNER, 1933; and Homolodromiinae ALCOCK, 1900. PATRULIUS (1959) introduced the Glaessneropsinae within the Prosopidae for *Glaessneropsis* PATRULIUS, 1959, taxa which GLAESSNER (1969) did not treat. cursory examination of the included genera leads to the conclusion that the family, as recognized by GLAESSNER and

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PATRULIUS, consists of a heterogeneous grouping. Allying seemingly unrelated taxa within a single family has the effect of obscuring phylogenetic relationships as well as making it difficult to consider ecological roles of the various taxa. As a result of this recognition, current studies by the authors, and others, have re-examined the fossil record of some of the genera within the Pithonotinae (sensu GLAESSNER 1969). The present work involves analysis of all genera within the Prosopinae (sensu GLAESSNER 1969) except *Laeviprosopon* GLAESSNER, 1933. These works employ a new combination of characters that permits more precise definition of generic characters and result in familial and generic definitions that embrace more homogeneous groupings.

Recent revisions have addressed the primarily Jurassic putative prosopid genera *Pithonoton*, *Goniodromites*, and *Nodoprosopon*, and have resulted in the recognition of new species, genera, and families (FELDMANN et al. 2006; SCHWEITZER et al. 2007; SCHWEITZER & FELDMANN 2008 [imprint 2007]). The genera within the Prosopinae sensu GLAESSNER (1969) have not yet been revised nor have the various species that have been placed over time within *Prosopon sensu lato*. Herein, we evaluate all of the species that at some time have been referred to *Prosopon*, *Nodoprosopon*, or *Lecythocaris*, and their family and generic level placement. The results of the study are four new families, four new genera, five new species, and eight new combinations (Table 1).

Table 1. Classification proposed herein.

<p>Superfamily Homolodromioidea ALCOCK, 1900</p> <p>Family Homolodromiidae ALCOCK, 1900</p> <p>See SCHWEITZER et al. 2004, for current list of included fossil genera</p> <p>Family Prosopidae VON MEYER, 1860 <i>sensu stricto</i></p> <p>Genus <i>Prosopon</i> VON MEYER, 1835 <i>sensu stricto</i></p> <p><i>Prosopon tuberosum</i> VON MEYER, 1840 (type species)</p> <p><i>P. abbreviatum</i> <b>new species</b></p> <p><i>P. aculeatum</i> VON MEYER, 1857</p> <p><i>P. mammillatum</i> WOODWARD, 1868</p> <p><i>P. verrucosum</i> REUSS, 1858</p> <p><i>P. ? dzhafarberdensis</i> (ILYIN, 2005)</p> <p>Genus <i>Protuberosa</i> <b>new genus</b></p> <p><i>Protuberosa protuberosa</i> (WEHNER, 1988) <b>new combination</b> (type species)</p> <p>Family Bucculentidae <b>new family</b></p> <p>Genus <i>Bucculentum</i> <b>new genus</b></p> <p><i>Bucculentum bucculentum</i> (WEHNER, 1988) <b>new combination</b> (type species)</p> <p><i>Bucculentum bachmayeri</i> <b>new species</b></p>
<p>Superfamily Glaessneropsoidea PATRULIUS, 1959 <b>newly elevated</b></p> <p>Family Glaessneropsidae PATRULIUS, 1959 <b>newly elevated</b></p> <p>Genus <i>Glaessneropsis</i> PATRULIUS, 1959</p> <p><i>Glaessneropsis heraldica</i> (MOERICKE, 1897) (type species)</p> <p><i>Glaessneropsis bucejana</i> PATRULIUS, 1959</p>

*Glaessneropsis myrmekia* **new species**

*Glaessneropsis tribulosa* **new species**

Genus *Verrucarcinus* **new genus**

*Verrucarcinus torosus* (VON MEYER, 1857) **new combination** (type species)

*Verrucarcinus ordinatus* (COLLINS *in* COLLINS and WIERZBOWSKI, 1985) **new combination**

Family Lecythocaridae **new family**

Genus *Lecythocaris* VON MEYER, 1858

*Lecythocaris paradoxa* (VON MEYER, 1858) (type species)

*Lecythocaris obesa* **new species**

Family Longodromitidae **new family**

Genus *Longodromites* PATRULIUS, 1959

*Longodromites angustus* (REUSS, 1858) (type species)

*L. bicornutus* MUȚIU & BĂDĂLUȚĂ, 1971

*L. excisus* (VON MEYER, 1857)

*L. ovalis* (MOERICKE, 1897)

Genus *Abyssophthalmus* **new genus**

*Abyssophthalmus spinosus* (VON MEYER, 1842) **new combination** (type species)

*A. mirus* (MOERICKE, 1897) **new combination**

*A. stotzingensis* (VON MEYER, 1856) **new combination**

Genus *Planoprosopon* SCHWEITZER et al., 2007

*Planoprosopon heydeni* (VON MEYER, 1857) (type species)

*Planoprosopon aequus* (VON MEYER, 1857) **new combination**

Family Nodoprosopidae **new family**

Genus *Nodoprosopon* BEURLEN, 1928

*Nodoprosopon ornatum* (VON MEYER, 1842) (= *N. ornatum carpaticum* PATRULIUS, 1966) (type species)

In nineteenth and early twentieth century works on these genera, features of the dorsal carapace such as grooves, regions, and ornamentation were utilized to classify Jurassic brachyurans. In the present paper, we place particular emphasis not only on these features but also on characteristics of the rostrum, orbits and their architecture, and subdorsal regions. By evaluating these features together, we have been able to separate the species into more unified and clearly related groups, rather than placing all of the heavily ornamented Jurassic brachyurans into one or a few genera as has been done previously.

WEHNER (1988) referred many genera that previously had been placed within *Prosopon* to *Foersteria* WEHNER, 1988, now *Gabriella* COLLINS & ROSS *in* COLLINS et al., 2006 (Table 2). The composition of *Gabriella* appears to be polyphyletic based upon our examination of type and other material at several museums, and the type species, *Gabriella biburgensis* (WEHNER, 1988), is clearly unrelated to any of the taxa discussed in this paper due to its poorly developed orbits and rostrum, relatively smooth carapace,

and rectangular shape. Work on that genus is underway but is beyond the scope of this paper. For now, we list those species of *Prosopon* that WEHNER (1988) placed within *Foersteria* (now *Gabriella*) as being members of *Gabriella*. Family placement for *Gabriella* is at this time unknown. In addition, we acknowledge that many Mesozoic genera have not yet been addressed, including *Laeviprosopon* GLAESSNER, 1933, as well as several genera within the Pithonotinae (*sensu* GLAESSNER 1969); investigation into those genera is ongoing.

Table 2. Species at one time referred to *Prosopon* that are treated herein; others recently have been revised and placed within other genera or families other than Prosopidae (see FELDMANN et al. 2006; SCHWEITZER et al. 2007; SCHWEITZER & FELDMANN 2008 [imprint 2007]). *Foersteria* WEHNER, 1988, was recognized as a junior homonym and was replaced by the name *Gabriella* (COLLINS and ROSS in COLLINS et al., 2006). Genera and species are arrayed by family, which are placed alphabetically after the Prosopidae in the last column on the right.

Species	Current Genus Designation	Reference	Current Family Designation
<i>Prosopon tuberosum</i> VON MEYER, 1860 (TYPE)	<i>Prosopon sensu stricto</i>	Herein	Prosopidae <i>sensu stricto</i>
<i>Prosopon aculeatum</i> VON MEYER, 1857	<i>Prosopon sensu stricto</i>	Herein	Prosopidae <i>sensu stricto</i>
<i>Prosopon mammillatum</i> WOODWARD, 1868	<i>Prosopon sensu stricto</i>	Herein	Prosopidae <i>sensu stricto</i>
<i>Prosopon verrucosum</i> REUSS, 1858	<i>Prosopon sensu stricto</i>	Herein	Prosopidae <i>sensu stricto</i>
<i>Prosopon protuberosum</i> WEHNER, 1988	<i>Protuberosa</i> new genus	Herein	Prosopidae <i>sensu stricto</i>
<i>Prosopon icaunensis</i> VAN STRAELEN, 1936	<i>Laeviprosopon fraasi</i> (MOERICKE, 1897)	WEHNER (1988)	Prosopidae <i>sensu lato</i>
<i>Prosopon bucculentum</i> (WEHNER, 1988)	<i>Bucculentum</i> new genus	Herein	Bucculentidae new family
<i>Prosopon schneideri</i> STOLLEY, 1924	<i>Oxythyreus</i> ?	Herein	Dynomenidae ORTMANN, 1892 <i>sensu lato</i>
<i>Prosopon villersensis</i> HÉE, 1924	<i>Heeia</i> WRIGHT & COLLINS, 1972	WRIGHT & COLLINS (1972)	Dynomenidae <i>sensu lato</i>
<i>Prosopon auduini</i> (EUDES- DESLONGCHAMPS, 1835)	Homolodromiidae incertae sedis	Herein	Homolodromiidae <i>sensu lato</i>
<i>P. mirum</i> MOERICKE, 1897	<i>Abyssosphthalmus</i> new genus	Herein	Longodromitidae new family
<i>P. spinosum</i> VON MEYER, 1842	<i>Abyssosphthalmus</i> new genus	Herein	Longodromitidae new family
<i>P. stotzingense</i> VON MEYER, 1856	<i>Abyssosphthalmus</i> new genus	Herein	Longodromitidae new family
<i>Prosopon angustum</i> REUSS, 1858	<i>Longodromites</i> PATRULIUS, 1959	PATRULIUS (1959)	Longodromitidae new family
<i>Prosopon excisum</i> VON MEYER, 1857	<i>Longodromites</i> PATRULIUS, 1959	PATRULIUS (1966)	Longodromitidae new family

Species	Current Genus Designation	Reference	Current Family Designation
<i>P. ovale</i> MOERICKE, 1897	<i>Longodromites</i> PATRULIUS, 1959	PATRULIUS (1966)	Longodromitidae new family
<i>Prosopon aequum</i> VON MEYER, 1857	<i>Planoprosopon</i> SCHWEITZER et al., 2007	Herein	Longodromitidae new family
<i>Prosopon heydeni</i> VON MEYER 1857	<i>Planoprosopon</i> SCHWEITZER et al., 2007	SCHWEITZER et al., 2007	Longodromitidae new family
<i>P. ordinatum</i> (COLLINS in COLLINS & WIERZBOWSKI, 1985)	<i>Verrucarcinus</i> new genus	Herein	Glaessneropsidae PATRULIUS, 1959
<i>P. torosum</i> VON MEYER, 1857	<i>Verrucarcinus</i> new genus	Herein	Glaessneropsidae PATRULIUS, 1959
<i>Prosopon lugobaensis</i> FÖRSTER, 1985	<i>Gabriella</i>	WEHNER (1988)	Incertae sedis
<i>Prosopon major</i> HÉE, 1924	<i>Gabriella</i>	WEHNER (1988)	Incertae sedis
<i>Prosopon hebes</i> VON MEYER, 1840	? <i>Gabriella</i>	Herein	Incertae sedis
<i>Prosopon circinatum</i> (COLLINS in COLLINS & WIERZBOWSKI, 1985)	Incertae sedis	Herein	Incertae sedis

A large collection of specimens, primarily from a collection of decapods from the Ernstbrunn Limestone in Austria, made by FRIEDRICH BACHMAYER, contains many specimens that preserve the anterior part of the dorsal carapace of several genera of prosopids. Typically, prosopids are tiny and are preserved as molds of the interior of the carapace. The frontal region is often broken away. Ventral surfaces and appendages have been found only once (von MEYER 1860, fig. 16) in association with the carapaces. As a result, classification of the group has relied largely upon morphology of the groove pattern and overall outline of the carapace. Study of the Ernstbrunn material, specimens collected by us and our colleagues in Romania, and material housed in several European museums has provided a sufficient number of specimens on which the rostrum and orbital region is preserved to document fundamental differences in architecture that provide important characters upon which to base a reclassification. Detailed definition of the differences of the structures will be discussed below; however, it is important to provide some generalizations in order to understand the magnitude of differences and their significance in classification (Fig. 1).

The rostral regions within the groups presently under consideration either exhibit three acuminate spines or are spatulate. The spatulate forms may be axially sulcate, axially ridged, or more or less flattened, and the entire rostrum may project forward or be strongly downturned.

The orbital structures vary widely. Some taxa lack well-defined orbital structures, whereas most have orbits or depressed regions in which the eye can rest. Many Jurassic Brachyura lack well-developed orbits, which we define herein as being circular or

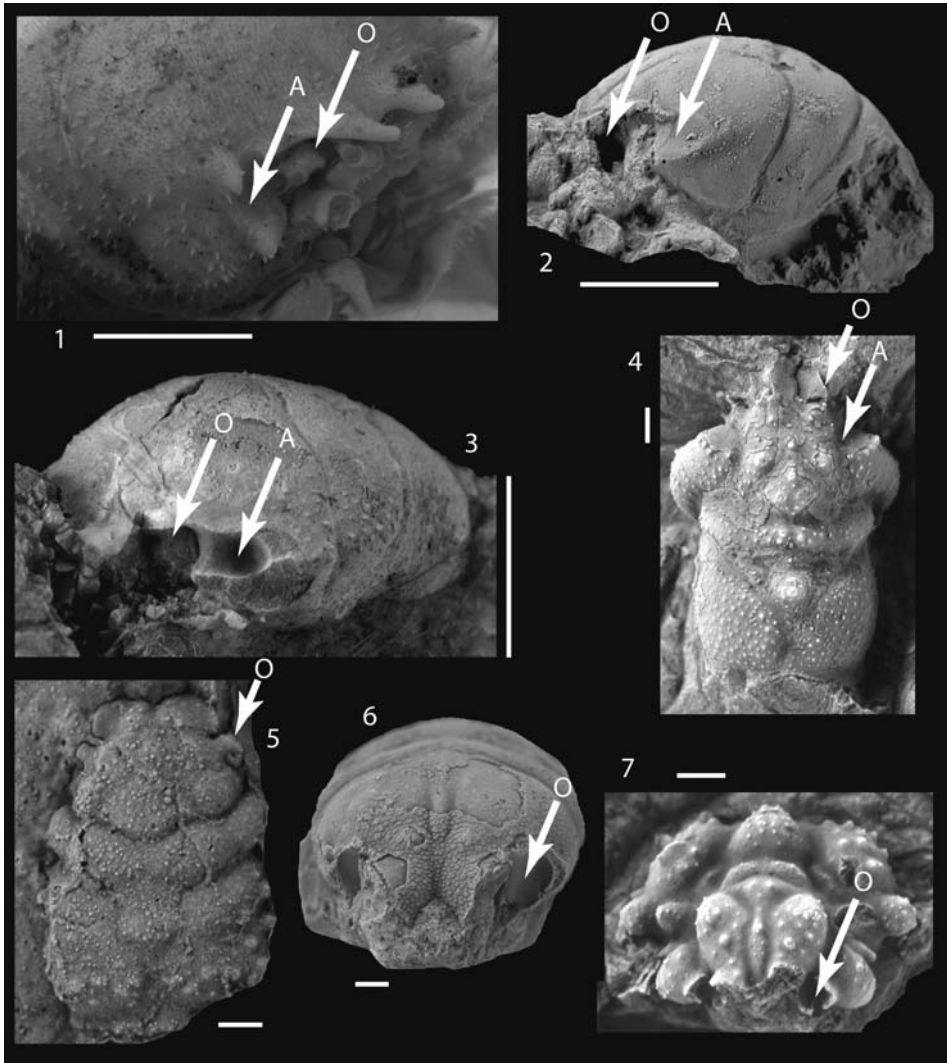


Fig. 1. Orbital structure in various Homolodromioidea (1-4) and Glaessneropsoidea (5-7). 1, *Homolodromia robertsi* GARTH, 1973, LACM CR 1980, 158.6, oblique anterior view, coastal Chile, Holocene; 2, *Tanidromites etalloni* (COLLINS in COLLINS & WIERZBOWSKI, 1985), IGPUW/1/10, holotype, cast, oblique anterior view, Raciszyn, Polish Jura, upper Oxfordian (Upper Jurassic); 3, *Pithonoton marginatum* VON MEYER, 1842, SMF x/m 190, oblique anterior view, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 4, *Bucculentum bachmayeri* new species, holotype, NHMW 1990/0041/3376, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 5, *Verrucarcinus torosus*, neotype, BSP 1881 IX 686, Oerlinger Tal, Germany, Upper Jurassic; 6, *Longodromites angustus*, NMHW 2007z0162/001, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 7, *Lecythocaris obesa* new species, paratype, NHMW 1990/0041/1330, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic). A = augenrest, o = orbit. Scale bars for 4, 5, 6, 7 = 1 mm; scale bar for 3 = 5 mm; scale bars for 1 and 2 = 1 cm.



elongate openings and sometimes depressions from which the eyestalk arises and then lies obliquely (Fig. 1). GUINOT & RICHER DE FORGES (1995: 304) referred to this structure as the *plage orbitaire* in the Homolidae DE HAAN, 1839. SCHWEITZER & FELDMANN (2008 [imprint 2007]) used the term “orbital socket” for this structure. The depression may be very elongate, as in many extant Portunidae or it may be absent as in extant Homolodromiidae, in which the orbit consists only of an opening for the eyestalk. This definition is intended to be consistent with current usage of the term “orbit” by neontologists and paleontologists in their taxonomic descriptions.

Many Jurassic Brachyura as well as extant Homolodromiidae possess a second structure associated with the orbits. SCHWEITZER & FELDMANN (2008 [imprint 2007]) referred to this structure as “a shallow depression” or simply as part of the orbit; however, examination of neontological literature suggests that the second structure is indeed unique and distinct. Herein we propose the term *augenrest* for this structure, derived from the German *auge* (plural, *augen*), meaning eye, and the English *rest*, referring to a resting place, because this structure houses the eye but is extralimital to the orbit (Fig. 1.1-1.4). In most taxa, it is composed of a circular or elongate cavity, often surrounded by a rim, spines, or both. It is separated from the orbit proper by a small ridge (Fig. 1.3) or a space (Fig. 1.4). The augenrest is seen in the Homolodromiidae, the Prosopidae, the Goniodromitidae BEURLEN, 1932, and the Tanidromitidae SCHWEITZER & FELDMANN, 2008 [imprint 2007], and the Bucculentidae nov. fam. described herein. We place all of these families within the Homolodromioidea based upon their possession of this unique feature. In addition, the orbital structures can be directed forward or anterolaterally and can be protected by suborbital swellings or eaves. The eaves may be entire or incised by deep notches.

Variations in rostral conformation and orbital architecture of these types are considered to be very important in classification of other groups of brachyurans, and, for that reason, are taken to be equally important in the classification of the prosopids. Similar points of variation recently have been used in reappraising some of the genera previously assigned to the Pithonotinae (*sensu* GLAESSNER 1969) (SCHWEITZER & FELDMANN 2008 [imprint 2007]).

#### *Key to extinct families defined herein:*

- 1a. Carapace lacking well-defined orbits or reentrants in which eye can rest; rostrum composed of three acuminate spines; carapace narrowing markedly anteriorly ..... Nodoprosopidae
- 1b. Carapace with well-defined orbits and/or augenrests, rostrum of varying shapes but not composed of three acuminate spines; carapace rectangular, ovate, or narrowing slightly anteriorly ..... 2
- 2a. Carapace with orbits and augenrests, rostrum may be small or projected well beyond orbit; cervical and branchiocardiac grooves usually equally developed ..... 3
- 2b. Carapace with orbits and lacking augenrests, rostrum usually large and spatulate, projected well beyond orbit; cervical and branchiocardiac grooves usually well defined but may not be of equal development ..... 6

- 3a. Augenrest on anterior margin of carapace, directed forward;  
branchial region marking widest point of carapace. . . . . 4
- 3b. Augenrest on hepatic region of dorsal carapace, directed vertically; protected by spines and ridges on the hepatic regions; hepatic region marking widest point of carapace. . . . . Bucculentidae
- 4a. Augenrest not protected by spines or swellings, developed as a groove on frontal margin of carapace, regions relatively uninflated, grooves deep. . . . . 5
- 4b. Augenrest protected by large suborbital swelling and supraorbital swellings, not developed as an elongate groove; regions bulbous, grooves usually deep . . . . . Prosopidae
- 5a. Augenrest shallow, directed forward or weakly anterolaterally, orbit separated from augenrest by distinct ridge; hepatic and antennar grooves well developed. . . . . Tanidromitidae
- 5b. Augenrest deep, directed anterolaterally, with or without low ridge separating orbit from augenrest at about two-thirds the distance distally. . . . . Goniidromitidae
- 6a. Cervical groove originating well posterior to position of outer-orbital spine, progressing in overall nearly straight path across carapace; area between cervical and branchiocardiac grooves narrow . . . . . Longodromitidae
- 6b. Cervical groove originating just posterior to outer-orbital angle or with poorly marked path; where path visible, may be sinuous or markedly concave forward; area between cervical and branchiocardiac grooves not markedly narrow or even well defined . . . . . 7
- 7a. Carapace triangular, with branchial regions extending markedly laterally; with well-defined grooves that include but are not limited to cervical, postcervical, and branchiocardiac grooves . . . . . Lecythocaridae
- 7b. Carapace longer than wide, with weakly inflated or uninflated branchial regions; with well-defined cervical and branchiocardiac grooves easily recognized. . . . . Glaessneropsidae

### Study Areas

The new species of brachyurans described herein were collected by FRIEDRICH BACHMAYER in the mid-twentieth century from a total of five localities of what is called the Ernstbrunn Quarry. The quarry localities are near the town of Dörfles in rocks of the Ernstbrunn Limestone. These localities are located north of Vienna. The Ernstbrunn Formation near Dörfles is middle to late Tithonian (latest Jurassic) in age based upon ammonite stratigraphy (ZEISS 2001; see map, p. 23, fig. 2). The formation extends into the earliest Cretaceous at other localities (ELIÁŠ 1992; ZEISS 2001). Fossils are well known from the unit, including algae (HOFMANN 1993), corals (ELIÁŠOVÁ 1990), ammonites (ZEISS 2001), and isopod crustaceans (BACHMAYER 1955), and there are preliminary reports of decapod crustaceans (BACHMAYER 1947; 1948). Herein we provide descriptions of several new species of brachyurans taken from the enormous collection



made by BACHMAYER at the Ernstbrunn quarries near Dörfles, housed in the Naturhistorisches Museum Wien, but never published. Study of his material is ongoing.

A small number of specimens referred to the new or previously described taxa were collected from the Štramberg locality in what is now the Czech Republic. This locality exposes the Štramberg Limestone (sometimes spelled Stramberg), which is composed of gray, fossiliferous limestone of Tithonian age (HOUSHA 1975; ELIAŠOVÁ 1981), determined on ammonite evidence (ELIAŠOVÁ 1981). The Štramberg Limestone is coral rich and serves as a model for other Jurassic limestones in eastern Europe. For example, throughout Poland and Romania, other limestone units are compared to the Štramberg Limestone and are called Štramberg-type limestones (MUȚIU & BĂDĂLUȚĂ 1971; KROBICKI et al. 2007) or Štramberg-reef facies (MÜLLER et al. 2000), indicating that they formed within coral-rich, reefal environments. It is beyond the scope of the present paper to comment on whether or not all of these limestones are truly analogous to the Štramberg Limestone; however, investigation of that hypothesis is ongoing, at least in terms of the hosted decapod faunas.

### Abbreviations

*Institutional abbreviations used throughout the work.* – BM, The Natural History Museum, London, UK; BSP, Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany; GSA, Geological Survey of Austria, Vienna, Austria; IGPUW, Institute of Geology, University of Warsaw, Poland; KSU D, Kent State University Decapod Comparative Collection; LACM, Natural History Museum of Los Angeles County, California, USA; LPBart, Laboratory of Paleontology, Department of Geology and Paleontology, University of Bucharest, Romania; NHMW, Naturhistorisches Museum Wien (Natural History Museum of Vienna), Austria; SM, Sedgwick Museum, Cambridge University, UK; SMF, Senckenberg Forschungsinstitut und Natur-Museum, Department of Paleontology and Historical Geology, Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany. Specimens in the collection of the Universitäts Museum Tübingen, Tübingen, Germany, are numbered according to the author, publication, year, and figure number and prefixed with the designation “Museum Tübingen.”

*Note on VON MEYER scale bars.* – VON MEYER (1860) placed scale bars in his illustrations. We attempted to determine the nature of these and through trial and error, ruled out inches and millimeters. There is no reference scale in the manuscript to which to compare the scales. The best suggestion we have received thus far is that the scales may refer to the actual size of the specimen (J. W. M. JAGT, personal communication, January, 2008), but that has not been confirmed by us.

*Validity of names.* – WEHNER (1988) is a Ph.D. dissertation. It was reportedly distributed among numerous libraries in Germany at the time it was finished, and in that country, this is considered to be a valid publication according to our interpretation of conversations that we had with several colleagues (G. SCHWEIGERT, M. NOSE, H. SUMMESBERGER, O. SCHULTZ, personal communication, June and July, 2006). Any misinterpretations of conversations with these colleagues are of course our responsibility. Many of the names subsequently were used (MÜLLER et al. 2000, for example) in valid publications. Ac-

According to the ICZN (1999), works published after 1985 and before 2000 must meet the criteria for works before that time if printed in a conventional means, which the work under consideration was. The criteria were thus that it must have been obtainable free of charge, be public and permanent, and be produced in multiple identical copies (ICZN 1999: 6-7). The dissertation met all of these criteria. Further, we consulted with two colleagues who have had many dealings with the International Commission of Zoological Nomenclature about the validity of the names published in WEHNER (1988). They agreed that the names erected in the dissertation were best treated as available (R. LEMAITRE, United States National Museum of Natural History and P. K. L. NG, National University of Singapore, personal communication, August and September, 2006, respectively). Indeed, we agree that this is the most parsimonious and easiest means of treating the work, the names, and the specimens, which are deposited in museums throughout Germany and Austria. Thus, in this, previous, and subsequent works, we treat names erected by WEHNER (1988) as available names.

### Systematic Paleontology

**Remarks:** The original generic names for many of the species discussed herein were either *Prosopon* or *Nodoprosopon*, both neuter in gender. Although *Lecythocaris* ends in *-is*, it is indeed feminine in gender. The new generic names are of varying genders; thus, the endings of the trivial names are changed to reflect the gender of the new genus to which they are referred herein.

#### Superfamily Homolodromioidea ALCOCK, 1900

**Included families:** Bucculentidae nov. fam.; Goniodromitidae BEURLIN, 1932; Homolodromiidae ALCOCK, 1900; Prosopidae VON MEYER, 1860; Tanidromitidae SCHWEITZER & FELDMANN, 2008 [imprint 2007].

**Diagnosis:** Podotrematous brachyurans with elongate-oval or rectangular carapace; with or without sharp margin between dorsal and lateral edges of carapace, lateral margins of carapace may be high, becoming less high in branchial region where cuticle may be uncalcified; carapace ornamentation often reduced, usually composed of small spines or nodes; cervical and branchiocardiac grooves about equally developed, postcervical groove usually present; *lineae homolicae* absent; orbit small, consisting of only an opening for the eyestalk, augenrest placed distal to the orbit to house the eye, orbital structures may or may not occupy entire frontal margin of carapace; rostrum ranging from small to projected well beyond orbits; with strong spine which can be compared to an antennal scale; pereopods 4 and 5 reduced, subchelate, elevated over the dorsal carapace to hold a protective structure for the carapace; thoracic sternum situated toward the rear, enlarged posteriorly, with suture lines but with zones of grooves and lateral expansions; without true sterno-abdominal cavity; male abdomen with seven somites incompletely fused, close proximity of the male abdomen with the coxae; uropods present but reduced and situated ventrally (adapted from GUINOT 1978; MARTIN 1990).

**Discussion:** To our knowledge, no succinct definition of the characteristics of the Homolodromioidea has been presented. GUINOT (1978) proposed the superfamily to

reflect the primitive nature of the Homolodromiidae, based upon possession of gills that were intermediate in grade between the trichobranchial forms known within lobster groups and the phyllobranchial form which is typical of brachyurans. Additionally, the presence of vestigial uropods (GUINOT 1978; MARTIN 1990) certainly suggests affinities, albeit distant, with the macrurans. These characters were judged by GUINOT to be sufficient to separate the Homolodromiidae from the families within the Dromioidea DE HAAN, 1833. MARTIN (1990) noted that the separation into a new superfamily was not widely accepted at that time, but MARTIN & DAVIS (2001) did recognize the Homolodromioidea. We concur. The presence of so many Mesozoic families within the superfamily, and the confirmed presence of members of the nominate family in the Cretaceous (SCHWEITZER et al. 2004) clearly indicates that it is a primitive group with a well-established fossil record extending from the Mesozoic to Recent.

Assignment of extinct families to the superfamily must be based solely upon characters of the dorsal carapace, at least thus far for the Jurassic groups. No ventral portions of the carapace or appendages have been recovered. Central to the placement of taxa into the superfamily is the architecture of the frontal region and the structures related to the orbits. The Homolodromioidea have orbits and augenrests to protect the eyes. In addition to the structures associated with the eyes, the absence of *lineae* and distinct lateral edges of the dorsal carapace and the presence of multiple transverse grooves and weakly calcified lateral flanks also unites the Jurassic forms and the extant homolodromiids. Variations of these latter features as well as variations in rostral form serve to distinguish taxa at the family level.

#### Family Prosopidae VON MEYER, 1860

Included genera: *Prosopon* sensu stricto; *Protuberosa* nov. gen.

**Diagnosis:** Carapace longer than wide, narrowing anteriorly, widest at branchial regions; regions well defined by grooves; cervical and branchiocardiac groove well developed; postcervical groove usually present; rostrum extending well beyond orbits; augenrest directed anterolaterally, bounded by inflated subhepatic region on suborbital rim and inner- and outer-orbital spine on upper-orbital margin; lateral margins well defined but not high; grooves deep and well marked, postcervical groove present; posterior margin bi-convex, apparently to accommodate fifth pereopods.

**Discussion:** The Prosopidae has had few formal definitions. GLAESSNER (1969: R484) diagnosed the family as being elongate, cylindrical, with or without a complete lateral margin, without true orbits but often with cavities to house the eye, and strong cervical and branchiocardiac grooves. He considered the Homolodromiidae to be a subfamily of the Prosopidae, a stance no others have taken although both families are generally now placed within the Homolodromioidea. GLAESSNER's (1969) diagnosis is essentially characteristic of members of the family as defined herein, although we add some details to assist in differentiating the family from other Jurassic groups. The nature of the orbital development in both *Prosopon* and *Protuberosa* differentiates the family from all others. The orbit is composed of a concave area defined by a variety of spines and swellings, not seen in other taxa. In addition, the biconcave nature of the posterior margin is unusual among the Jurassic brachyurans. Thus, the family is well constrained.

ILYIN (2005) described and illustrated a new species of *Nodoprosopon*, *N. dzhafarberdensis*. Examination of the illustrations of that species (text-fig. 35, pl. 7, fig. 3) suggests that it may be better placed within *Prosopon*. The granular ornamentation, long intestinal region, and deep grooves all suggest possible placement in *Prosopon*. However, examination of the holotype or a translation of the Russian text will be necessary to confirm the placement.

*Prosopon auduini* EUDES-DESLONGCHAMPS, 1835, was synonymized with *Prosopon longipes* WOODWARD, 1865 (HÉE 1924). WEHNER (1988) later referred it to *Gabriella* (= *Foersteria* in her work). The specimens referred to this species, as illustrated by HÉE (1924) and as seen in BM In. 57979, a paralectotype according to MORRIS (1980), have very well-developed, circular concavities in which the eye can rest that are ornamented with large spines. The rostrum is triangular with swollen areas on either side of the base, and the specimen lacks *lineae homolicae*. Thus, the species seems to be allied with members of the Homolodromiidae. However, detailed study of the paralectotype will be necessary to determine a generic and familial placement for the species. It is not a member of *Gabriella* because members of the type species of that genus do not possess well-developed orbits or concavities on the dorsal carapace in which the eye can rest.

SCHWEIGERT (2006) recorded a new specimen of *Prosopon hebes* VON MEYER, 1840. That species cannot be accommodated within *Prosopon* as restricted herein, based upon its lack of a biconcave posterior margin and rectangular shape. SCHWEIGERT (2006) mentioned possible affinities with *Gabriella* (= *Foersteria*) and *Prosopon spinosum* VON MEYER, 1842, which is herein referred to a new genus. It seems likely that the affinities of *P. hebes* lie with one of these latter mentioned taxa; however, original material will need to be examined to confirm the placement of *P. hebes*.

COLLINS in COLLINS and WIERZBOWSKI (1985) described *Prosopon circinatum* from Jurassic rocks of Poland. Examination of the holotype (IGPUW/C/1/1) indicates that the species is longer than wide, widest at about the mid-branchial region, and ornamented with numerous large tubercles. It has reasonably well-developed cervical and branchiocardiac grooves. Overall, the carapace is reminiscent of members of the Nodoprosopidae nov. fam. and the Glaessneropsidae PATRULIUS, 1959, described below, but it is unlike either in possessing a large, inflated epibranchial region with a small extension directed at the cardiac region. Unfortunately the entire front, rostrum, and orbital area of the carapace of the holotype and best-preserved specimen are missing. Thus, the species is placed as *incertae sedis* for now until more complete material can be recovered.

WEHNER (1988) synonymized *Prosopon icaunensis* VAN STRAELEN, 1936, with *Laeviprosopon fraasi* (MOERICKE, 1897). For now, we accept the synonymy; investigation of the composition and the definition of *Laeviprosopon* as well as its familial placement are ongoing. We refer it to the Prosopidae sensu lato for now, following GLAESSNER (1969). STOLLEY (1924) described *Prosopon schneideri*; however, the ovate carapace and scalloped margins visible in an unnumbered specimen in BSP (cast is KSU D 589) and in the illustrations of STOLLEY (1924: pl. 13, fig. 1) strongly suggest placement in *Oxythyreus* REUSS, 1858, to which we questionably assign it until type material can be examined. WRIGHT & COLLINS (1972) have already transferred *Prosopon villersensis* to *Heeia* WRIGHT & COLLINS, 1972, with which we concur.

Genus *Prosopon* VON MEYER, 1835 *sensu stricto*

Type species: *Prosopon tuberosum* VON MEYER, 1840, by original designation.

Other species: *Prosopon abbreviatum* nov. spec.; *P. aculeatum* VON MEYER, 1857; *P. mammillatum* WOODWARD, 1868; *P. verrucosum* REUSS, 1858.

Diagnosis: Carapace longer than wide, widest at about mid-branchial region; regions well defined by grooves and composed of greatly inflated swellings; cervical groove concave forward; branchiocardiac groove sinuous; postcervical groove deep, where present; mesogastric region overall triangular, composed of three large swellings arranged in a triangular shape; intestinal region long, narrow, distinct; sub-branchial region well developed when present; posterior margin biconcave, widely rimmed.

Discussion: WEHNER (1988) restricted the genus severely and we have largely followed her lead. The referred species other than the type species differ in some ways from the type species. For example, each of the other referred species possesses a postcervical groove, which is not apparent in the illustrations or in the description of *Prosopon tuberosum*. In addition, *P. tuberosum* possesses an inflated sub-branchial region that seems to be differentiated from the epibranchial region; this feature is present in some of the referred species but not all. Another factor is that VON MEYER reported *P. tuberosum* as Neocomian in age, whereas all of the other species are Late Jurassic in age. This is a difference in age of approximately 15 million years. Generic ranges extending from the Jurassic into the Cretaceous are not unknown for Mesozoic brachyurans (i.e. *Goniodromites* REUSS, 1858, from Late Jurassic [Oxfordian] to Late Cretaceous [Cenomanian]) (SCHWEITZER & FELDMANN 2008 [imprint 2007]), but they are by no means common.

The single most problematic factor concerning the nature of the genus *Prosopon* is that the type specimen of the type species has apparently been lost or destroyed. Inquiries at numerous institutions in Strasbourg, France, confirm that such a specimen is no longer extant in collections there. Additionally, the type specimen has not been found in any other museum in Germany or France. Thus, we are left with the written description and illustrations. REUSS (1858) described *P. verrucosum* as being similar in nature to *P. tuberosum*. Examination of the type specimen of *P. verrucosum* indicates that there are some differences between it and *P. tuberosum*, including lack of a well-separated sub-branchial region in *P. verrucosum* and presence of a well-developed postcervical groove in *P. verrucosum*. However, *P. verrucosum* demonstrates a biconcave posterior margin; well-defined carapace regions; deep cervical and branchiocardiac grooves; a bilobed metabranchial region; and protogastric and hepatic regions with numerous inflations, all of which are seen in *P. tuberosum*. Although there do appear to be some major differences between the carapace of *P. tuberosum* with *P. verrucosum* and several other species that have previously been referred to *Prosopon* (i.e., *P. aculeatum*), it seems imprudent at this time to erect a new genus for the other species in light of the facts that the type specimen of *P. tuberosum* is missing; VON MEYER's descriptions are not overly detailed; and his illustrations were sometimes exaggerated. Thus, we refer species with the general form of *P. verrucosum* to *Prosopon* at this time until type material for *P. tuberosum* can be found to better define the concept of the genus. What this will mean, of course, is that the general concept of *Prosopon* will at this time remain that of the morphology of *P. verrucosum* and *P. mammillatum*, as the original types for those species survive and there are numerous other examples of each species.



***Prosopon tuberosum* VON MEYER, 1840**

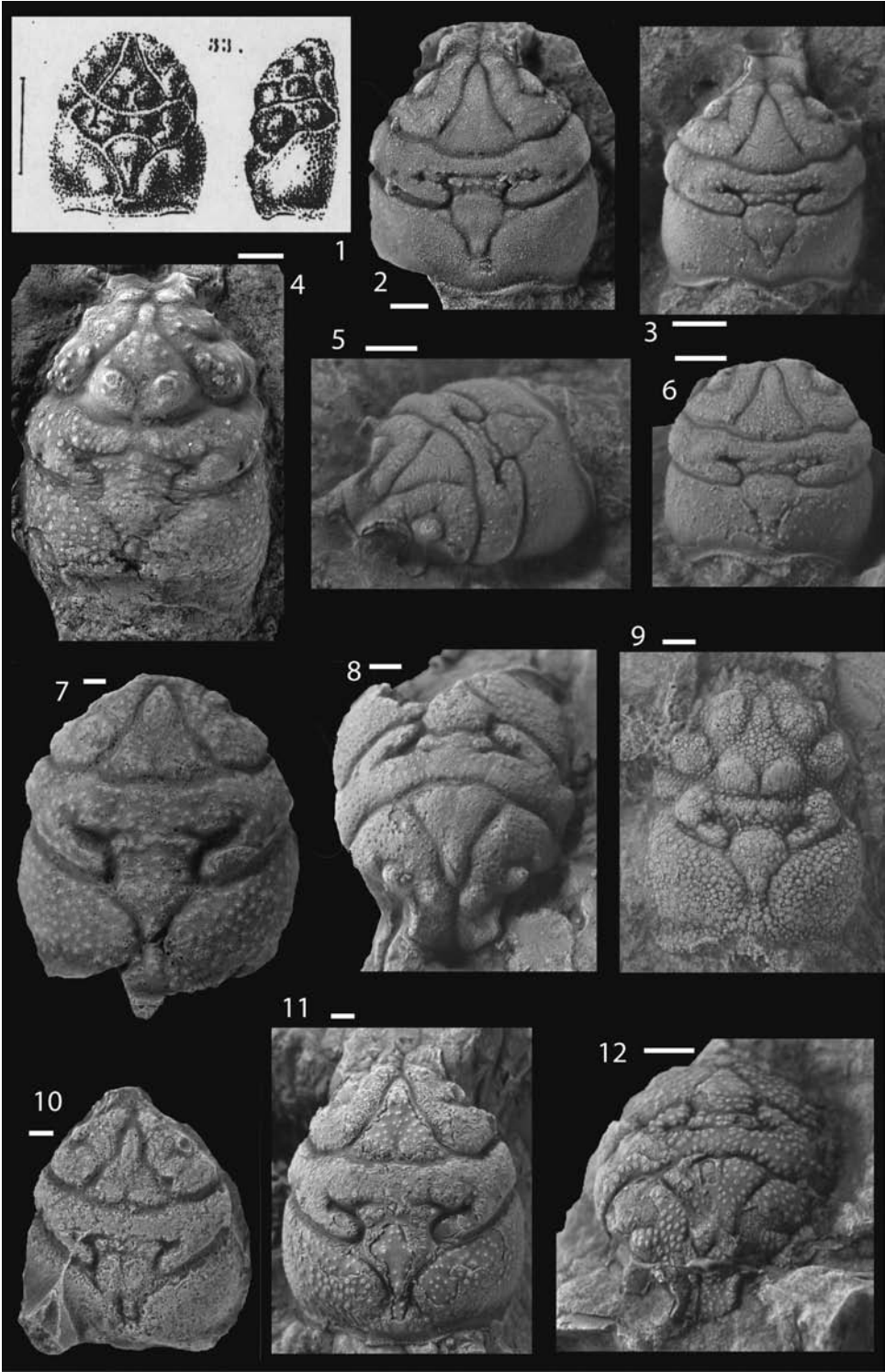
Fig. 2.1

- 1840 *Prosopon tuberosum* VON MEYER, p. 21, pl. 4, fig. 31.  
 1860 *Prosopon tuberosum* – VON MEYER, p. 216, pl. 23, fig. 33.  
 1928 *Pros. tuberosum* & *P. tumberosum* – BEURLIN, p. 146.  
 1929 *P. tuberosum* VON MEYER – GLAESSNER, p. 346.  
 1933 *Prosopon tuberosum* v. MEY. – GLAESSNER, p. 180.  
 1969 *P. tuberosum* VON MEYER – GLAESSNER, p. R484, fig. 294.1.  
 1988 *Prosopon tuberosum* VON MEYER – WEHNER, p. 25.  
 2000 *Prosopon tuberosum* VON MEYER – MÜLLER et al., p. 51.

**Description** (translated from German, VON MEYER 1860: 216; additions from illustrations added in square brackets): “The cephalothorax is 0.011 long, 0.009 wide (units for these measurements are unknown) [L/W=1.22], and 0.0055 high; the maximum width falls in the hind half [about 60 percent the distance posteriorly]. The front part is rounded. The regions are sharply defined and projected into protuberances. On the gastric region which leads up to the barely incised anterior end sits a short spine and it is taken in by three rounded, massive tubercles, corresponding to the corners of a triangle; of these, the hind pair is the strongest; in the back the gastric region measures less than half the length of the cephalothorax. The hepatic region consists on each side of three pairs of tubercles; of these the front is the weaker, and one notices also on the border similar tubercles. In the front transverse groove [cervical groove] lies a pair of pores. The genital region exhibits on the margin a tubercle and in the back a pair of tubercles, adjacent to whose posterior exterior edge a depressed point is formed. Between this pair of tubercles and the other tubercle lies a similar tubercle-formed swelling, with which the tubercle that is directed toward the cardiac region is fused. The cardiac region, which is in the front half inflated into a tubercle form, is shaped as an equilateral triangle with convex anterior sides. The inflated branchial region, which measures half the length of

Fig. 2. Prosopidae. 1, *Prosopon tuberosum*, digital image from VON MEYER (1860: pl. 23, fig. 33); 2, *Prosopon abbreviatum* new species, paratype, NHMW 2007/0149/0006, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *Prosopon abbreviatum*, holotype, NHMW 1990/0041/2487, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 4, *Prosopon mammillatum*, cast of holotype, SM B2719, Oxfordshire, England, Bathonian (Middle Jurassic); 5, *Prosopon abbreviatum*, paratype, NHMW 2007/0149/0006, oblique view showing orbit and suborbital spine, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 6, *Prosopon abbreviatum*, paratype NHMW 1990/0041/345, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 7, *Prosopon verrucosum*, cast of holotype, GSA 2360, Štramberg Limestone, Czech Republic, Tithonian (Upper Jurassic); 8, *Prosopon verrucosum*, NHMW 1990/0041/4059, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 9, *Protuberosa protuberosa* new combination, cast of holotype BSP SYL-1, Saal bei Kelheim, southern Germany, Kelheimer Schuttkalke, Jurassic; 10, *Prosopon aculeatum*, cast of neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 34, Oerlingen bei Ulm, Germany, Upper Jurassic; 11, *Prosopon verrucosum*, NHMW 2007/0149/0005, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 12, *Prosopon verrucosum*, NHMW 1990/0041/33, oblique anterior view showing rostrum and suborbital spine, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars = 1 mm except for Fig. 2.4 where scale bar = 5 mm. ►





the cephalothorax, is two times more strongly vaulted in the vicinity of the posterior transverse groove [branchiocardiac groove]. The posterior margin is therefore with two weak incisions not in the middle, but on the contrary, farther toward the outside, and bordered with a broad furrow. On the shell are scarcely any perceptible warts, those here and there and on the sides of the sharp furrows are distinct and prominent, on the branchial regions toward the outer margin they are most distinct and numerous.

From the “ferruginous oolite of the inferior Cretaceous stage,” Neocomian of Boucherans, in the French Department of Jura. There is only this one example known to me, a complete cephalothorax, which is preserved in the collection of the Académie of Strassburg.”

**Type:** According to WEHNER (1988), the type specimen is lost. We similarly have been unable to locate the type specimen or any other material of similar age that fits the description and illustrations (pl. 23, fig. 33, composed of two views) of VON MEYER (1860). The paleontological collections at the Université LOUIS PASTEUR in Strasbourg, France, have experienced several subdivisions, especially during the two world wars, and a major fire in 1967 in which 95 percent of the type and figured collection was destroyed (J. HORRENBERGER, personal communication, September, 2007). Thus, at this time, the type specimen of *Prosopon tuberosum* has not been located in the collections in Strasbourg. It is possible that the specimen was sent to a repository in Germany during one of the wars, but thus far no one has found it in any institution there.

**Discussion:** VON MEYER's 1860 description focused most markedly on the nodose nature of the carapace and the many inflated regions that are developed and well marked by grooves. He also noted that the posterior margin was biconvex, possibly to accommodate the fifth pereopods, and that the specimen was missing the rostrum. Examination of the illustrations in VON MEYER's 1860 work and careful reading of the 1860 description indicate that *Prosopon tuberosum* is in some ways unlike almost all other species that have subsequently been referred to *Prosopon*. First, VON MEYER illustrated an inflated region lateral to the well-described axial and epigastric regions, termed here a sub-branchial region (Fig. 2.1). This sub-branchial region is well seen in his side view (Fig. 2.1). The cervical groove has a short groove extending posteriorly and longitudinally from it, bounding the lateral edge of the metagastric region (Fig. 2.1). There does not appear to be a postcervical groove. Unfortunately, the only known illustration is the original from VON MEYER (1840), which has been repeated by subsequent authors (VON MEYER 1860; GLAESSNER 1969). In spite of these differences, we elect to retain the species listed above within *Prosopon*, especially in light of the apparent loss of the type specimen for *P. tuberosum*.

### ***Prosopon mammillatum* WOODWARD, 1868**

Fig. 2.4

**Diagnosis:** The species has been well described previously (WOODWARD 1868; WITHERS 1951), and it need not be repeated here.

**Material examined:** SM B2719, holotype; BM In. 44291, BM In. 596614; BM In. 28821.

**Discussion:** *Prosopon mammillatum* differs from other species in the genus in having shallower grooves and therefore more poorly defined regions. However, the

disposition of the regions and grooves is the same as in all other species of the genus; thus, it remains within the genus. *Prosopon mammillatum* is unique among members of *Prosopon* in possessing preserved eyestalks. The eyestalks are rather long and would have lain in the augenrest as seen in other species of the genus; however, augenrests are not preserved in *P. mammillatum*.

***Prosopon verrucosum* REUSS, 1858**

Figs. 2.7, 2.8, 2.11, 2.12

- 1858 *Prosopon verrucosum* REUSS, p. 11.
- 1859 *Prosopon verrucosum* n. sp. – REUSS, p. 70, pl. 24, fig. 1.
- 1860 *Prosopon verrucosum* – VON MEYER, p. 217.
- 1897 *Prosopon verrucosum* REUSS – MOERICKE, p. 62.
- 1924 [imprint 1925] *Prosopon verrucosum*, REUSS – VAN STRAELEN, p. 372.
- 1929 *P. verrucosum* REUSS – GLAESSNER, p. 347.
- 1933 *Pr. verrucosum* REUSS – GLAESSNER, p. 180.
- 1988 *Prosopon verrucosum* REUSS – WEHNER, p. 22.

**Original description** (translated from REUSS 1859: 70; additions from illustrations and examination of the holotype in square brackets): “Resembling closely *Prosopon tuberosum* VON MEYER, from the Neocomian of Boucherans in the Département du Jura; however, indeed it is different from it. The 0.66” length and 0.55” [L/W = 1.2] wide cephalothorax maintains in its posterior two-thirds an equal width, with rather parallel lateral margins; the front third is narrowed very rapidly and stretched in a somewhat downward-inclined spine, with a medial longitudinal groove. [Carapace widest about 70 percent the distance posteriorly on carapace; maximum width of mesogastric region about half maximum carapace width.] The shallow orbits are very closely spaced.

The surface of the carapace is divided by two transverse grooves into three distinct segments lying one behind the other. The anterior groove progresses in its middle part transversely, whereas the lateral segments of the posterior are directed obliquely toward the posterior and axially and in the middle meet below a sharp angle. The anterior segment of the cephalothorax is divided through two long, posteriorly diverging grooves into a middle posterior part and two lateral parts. The former [mesogastric region] appears as almost an equilateral triangle with each side weakly inflexed and is occupied by three tubercles arranged in the shape of a triangle, of which the most anterior is most strongly prominent. Each of the lateral regions [protogastric regions] also carries three, but longitudinally arranged, tubercles. The posterior-most of these is wide and large but flat; the other two are very small, nevertheless advancing sharply forward. The forward-most, smallest lie beside one another directly on the spine of the front region. All of these tubercles are through deep but narrow grooves separated from one another.

The middle part of the dorsal carapace extends in the middle far toward the posterior. The cardiac region is separated as a small distinct pentagonal field with a long dagger-like posterior spine. Especially the front side part [epi- and metabranchial?] is defined by a deep furrow. In front of the cardiac region lies a very shallow, saddle-shaped depression [probably urogastric region], through which it passes into the similarly raised front middle region [metagastric?]. [Metagastric region very large, wider than mesogas-

tric region, defined on anterior margin by cervical groove and posterior margin by postcervical groove. Urogastric region narrow, short, depressed below level of other axial regions.] Also the side part is rather similarly vaulted, without especially prominent tubercles; only from the front lateral summit of the aforementioned pentagonal field a short, very deep furrow [postcervical groove] stretches itself obliquely anterolaterally, just as in the case of many *Dromiopsis*-species.

The hind part of the cephalothorax shows only a very small middle region which can be viewed as a continuation of the posterior prolongation of the middle section of the carapace [intestinal region], from which it is only separated by a weak, short, transverse furrow. It forms a very small equilateral triangle with a posteriorly-directed base [intestinal region]. The largest part of the hind carapace embraces both lateral regions, which present a weakly similar vault without noteworthy tubercles present [metabran- chial regions].

The vault of the entire cephalothorax longitudinally is slight; only the front part curves somewhat strongly downward toward the rostrum. Much more significant is the convexity in the direction of the width. The posterior border of the carapace is long, both sides somewhat splayed out and with a narrow, raised rim. The shell is not preserved. However, on the whole upper surface of the steinkern are displayed dense, small, warty tubercles."

**Type:** The holotype, GSA 2360, was collected from the Štramberg locality.

**Description** of non-type, referred material: Carapace longer than wide, width about 85 percent maximum length including rostrum, maximum width usually positioned in branchial region about 70 percent the distance posteriorly but may be at epibranchial region about half the distance posteriorly; carapace moderately vaulted transversely, flattened longitudinally except in anterior one-third where it is deflexed; regions well marked by grooves, granular.

Rostrum long, initially straight sided, rim paralleling lateral sides, converging into triangular tip distally, deflexed, axially sulcate. Orbit arising from directly under rostrum; augenrest large, bi-concave, bounded by three orbital spines; suborbital spine flattened, with outer triangular projection; inner orbital spine small; outer orbital spine triangular, marking end of anterior margin of carapace. Subhepatic region elongate, bearing sub-orbital spine, bounded on posterior margin by posteriorly directed ventral extension of cervical groove and ventrally by antennar groove. Lateral margins of carapace bulbous between constrictions where cervical and branchiocardiac grooves intersect margin. Posterior margin biconcave, widely rimmed.

Epigastric regions rectangular, inflated. Protogastric regions composed of two lobes, one small and possessing inner orbital spine, second larger and possessing outer orbital spine; both granular. Mesogastric region with long anterior process that terminates between epigastric regions, process with elongate swelling; region widening posteriorly, composed of two lobes with posterior constriction between them. Metabran- chial region wide, bounded anteriorly by cervical groove and posteriorly by postcervical groove. Urogastric region short, narrow, anterior margin bounded by convex-forward segments of postcervical groove, lateral margins converging posteriorly, posterior margin convex forward. Cardiac region elongate, pentagonal, tip directed posteriorly, with two small swellings anteriorly. Intestinal region triangular, apex directed anteriorly.

Cervical groove initially deep, extending in deep concave arcs from lateral margin axially, then arcing around posterior margin of mesogastric region, overall path relatively straight. Postcervical groove discontinuous, composed of two short, sinuous arcs on either side of axis bounding posterior margin of metagastric region. Branchiocardiac groove deep laterally, extending obliquely posteriorly, then diverging strongly posteriorly to bound cardiac region. Epibranchial region strongly inflated laterally, narrowing into fingerlike projection axially which is bounded by postcervical and branchiocardiac grooves. Remainder of branchial region undifferentiated, bulbous. Sub-gastric regions appearing to be flattened. Epibranchial region inflated in lateral view but not forming separate sub-branchial region.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Prosopon verrucosum* are presented in Table 3.

Table 3. Measurements (in mm) taken on the dorsal carapace of *Prosopon verrucosum* collected from the Ernstbrunn quarries and deposited in NHMW. L1 = maximum carapace length; W1 = maximum carapace width; L2 = length to position of maximum width; W2 = maximum mesogastric width; W3 = rostral width.

Specimen	L1	W1	L2	W2	W3
NHMW 2007/0149/0005	15.0	12.9	10.4	5.9	4.2
NHMW 1990/0041/2516	5.4	4.7	3.8	1.9	2.2
NHMW 1990/0041/4908	2.5	1.9	-	0.7	-
NHMW 1990/0041/3961	9.7	8.2	6.8	3.6	-
NHMW 1990/0041/2520	8.9	7.5	6.3	2.9	2.6
NHMW 1990/0041/4059	7.9	6.7	4.8	2.9	2.5
NHMW 2007/0149/0003	15.6	13.7	10.4	6.0	-
NHMW 2007/0149/0004	7.1	6.6	3.3	3.0	-
NHMW 1990/0041/3756	4.8	3.7	2.6	1.6	-

**Material examined:** NHMW 1990/0041/33, NHMW 1990/0041/34, NHMW 1990/0041/1690, NHMW 1990/0041/2516, NHMW 1990/0041/2520, NHMW 1990/0041/3077, NHMW 1990/0041/3205, NHMW 1990/0041/3756, NHMW 1990/0041/3850, NHMW 1990/0041/3961, NHMW 1990/0041/4059, NHMW 1990/0041/4908, NHMW 2007/0149/0003, NHMW 2007/0149/0004, and NHMW 2007/0149/0005, in addition to the holotype listed above.

**Occurrence:** All of the material except the holotype was collected from the Ernstbrunn quarry localities.

**Discussion:** The material described here from the Ernstbrunn localities is referred to *Prosopon verrucosum* based upon its possession of a long metagastric region, biconcave posterior margin, granular regions, bulbous carapace shape, and broad branchial and epibranchial regions. Especially the long metabranchial region of the Ernstbrunn material excludes it from *Prosopon aculeatum*, discussed below.

The description of the Ernstbrunn material is maintained separately from REUSS's original description and observations from the holotype, because there are a few notable differences between the Ernstbrunn material and the holotype. In addition, the holotype



was collected from the Štramberg locality in what is now the Czech Republic, a different locality than the Ernstbrunn material. The Ernstbrunn specimens are characterized by possession of a cervical groove that is somewhat more sinuous than that seen on the holotype, and the holotype displays less distinctly differentiated urogastric and cardiac regions than those seen in the Ernstbrunn material. However, we regard those as intraspecific differences here, as the overall similarity of the material with the holotype is great.

***Prosopon aculeatum* VON MEYER, 1857**

Fig. 2.10

- 1857 *Prosopon aculeatum* VON MEYER, p. 556.
- 1860 *Prosopon aculeatum* – VON MEYER, p. 211, pl. 23, fig. 24.
- 1924 [imprint 1925] *Avihomola aculeata* VON MEYER – VAN STRAELEN, p. 342.
- 1925 *Prosopon aculeatum* H. v. MEYER – BEURLEN, p. 485.
- 1928 “Avih.” *aculeata* zu *Prosopon* s. st. – BEURLEN, p. 149.
- 1929 *P. aculeatum* v. MEYER – GLAESSNER, p. 341.
- 1933 *Pr. aculeatum* v. MEYER – GLAESSNER, p. 180.
- 1988 *Prosopon aculeatum* VON MEYER – WEHNER, p. 17, pl. 1, figs. 1, 2.
- 2000 *Prosopon aculeatum* VON MEYER – MÜLLER et al., 2000, fig. 17A.

**Original description** (translated from German, VON MEYER 1860: 211; additions from illustrations added in square brackets): “I know of only one specimen, however perfectly sufficient, to permit recognizing the characteristic shape of the species. The cephalothorax is 0.0115 (units of these measurements unknown) long. Of this the front part takes in less than half and is thereby less wide as long; the width attains almost 0.0075. The sharply delimited gastric region is as long as wide, its short anterior projection ends a definite distance from the front end and possesses a weak groove-formed impression; posteriorly, the gastric region is weakly notched. The front end of the cephalothorax is stubby and weakly incised, giving rise to projecting sharp corners. The hepatic region is provided with two strong warts situated toward the gastric region along the inner margin of the hepatic region, the forward one arises in the vicinity of the anterior process of the gastric region; more toward the lateral edges of the hepatic region lie two spines. In the posterior [we believe that he meant anterior] transverse groove are recognized the indication of a pair of pores. The middle part gives to the front part in size nothing toward [we believe this to mean that the middle part is the same width as the anterior]. In the middle part the cephalothorax reaches 0.009 wide, especially through an outer lying sharp hump. The oblique mounds directed toward the cardiac region on each side are not separated from the genital region. A pair of mounds is perceived directly in front of the cardiac region which are small, lying near together, and maintain the opposite orientation and appear directed towards the posterior and outside. It might be possible, that they only are presented front angles of the cardiac region, which then is approximately once more as long as wide when the hind spine is taken in addition. The hind part of the cardiac region appears with three tubercles arranged into a triangle. Judging by the incompletely preserved right half of the branchial region, the left half is judged to appear diseased and inflated; in the healthy cephalothorax the width in this region will not have been under 0.01. Thereby the posterior part did not attain half the length of the cephalothorax, and is decorated with small warts, which probably are also on other regions more



or less clearly perceived. Posteriorly, the middle region of the cephalothorax is more clearly incised and the margin is hardly surrounded with a furrow.

From the upper white Jurakalk of the Oerlinger Thals, in WETZLER's collection."

**Material examined:** Neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 34, collected from the Oerlinger Thals, near Ulm, Germany; BSP 1988 I 19, collected from Unterwilflingen northwest of Nördlingen, Germany.

**Discussion:** WEHNER (1988) designated a neotype, from the type locality, for *P. aculeatum*, which is now deposited in the Museum Tübingen (MÜLLER et al. 2000: fig. 17A). WEHNER (1988) also identified BSP 1988 I 19 as *P. aculeatum*. Both of these specimens agree well with the 1860 description of VON MEYER. *Prosopon aculeatum* is differentiated from *P. verrucosum* because *P. verrucosum* has a much longer metagastric region than does *P. aculeatum* and *P. aculeatum* possesses marked, acute nodes on the protogastric regions which *P. verrucosum* lacks.

***Prosopon abbreviatum* nov. spec.**

Figs. 2.2, 2.3, 2.5, 2.6

**Diagnosis:** Carapace slightly longer than wide, width about 90 percent carapace length including rostrum; regions well marked by grooves, ornamented with scattered tubercles, generally flattened and not inflated; epigastric regions rectangular, weakly inflated; mesogastric region broadly triangular, terminating between epigastric regions, without particular swellings; urogastric region very short; cardiac region rounded-triangular, apex directed posteriorly, without swellings; intestinal region poorly developed as a thickening in cuticle.

**Description:** Carapace slightly longer than wide, width about 90 percent carapace length including rostrum, widest at branchial regions about two-thirds the distance posteriorly on carapace or at epibranchial region, about half the distance posteriorly; regions well-marked by grooves, ornamented with scattered tubercles, generally flattened and not inflated.

Rostrum straight sided proximally, rimmed, weakly converging distally into triangular tip; orbit arising from under rostrum. Augenrest biconcave, ornamented with spines; suborbital spine flattened, with broad triangular lateral projection; inner orbital spine with large, rounded base, short; outer orbital spine triangular, directed anterolaterally, marking outer edge of anterior margin of carapace.

Lateral margins of carapace strongly convex between cervical and branchiocardiac grooves, weakly inflated posterior to branchiocardiac groove. Posterior margin biconcave, rimmed.

Epigastric regions rectangular, weakly inflated. Protogastric regions broad, with orbital spines on margins. Mesogastric region broadly triangular, terminating between epigastric regions, without particular swellings. Metagastric region short, wide, bounded anteriorly by cervical groove, posteriorly by segments of postcervical groove. Urogastric region very short. Cardiac region rounded-triangular, apex directed posteriorly, without swellings. Intestinal region poorly developed as a thickening in cuticle.

Cervical groove composed of three concave-forward segments bounding protogastric regions and metagastric region, overall shape convex forward. Postcervical groove discontinuous, deep. Branchiocardiac groove directed weakly posteriorly and axially, deepest laterally, weakly diverging posteriorly to outline cardiac region.

Epibranchial region composed of lateral lobe which is moderately inflated and axially of fingerlike projection bounded by postcervical and branchiocardiac grooves. Remainder of branchial region undifferentiated, flattened, not inflated.

**E t y m o l o g y :** The trivial name is the Latin word *abbreviatum*, meaning shortened, referring to the shortened nature of the metagastric and urogastric regions of the carapace as well as the overall shortness of the carapace with respect to the maximum width.

**M e a s u r e m e n t s :** Measurements (in mm) taken on specimens of *Prosopon abbreviatum* nov. spec.: NHMW 2007/0179/0006, maximum carapace length, 10.7; maximum carapace width 9.6; length to maximum width 7.2; NHMW 1990/0041/345, maximum carapace length >3.6; maximum carapace width, 3.8; NHMW 1990/0041/2487, maximum carapace length, 4.3; maximum carapace width, 3.7; length to maximum width, 1.9; rostral width, 1.4.

**T y p e s :** The holotype, NHMW 1990/0041/2487, and two paratypes, NHMW 1990/0041/345, NHMW 2007/0179/0006.

**O c c u r r e n c e :** The specimens were collected from the Ernstbrunn quarry localities.

**D i s c u s s i o n :** The flattened carapace regions and the nearly equant shape of the carapace distinguish the new species from all other species within the genus.

### Genus *Protuberosa* nov. gen.

**T y p e s p e c i e s :** *Prosopon protuberosum* WEHNER, 1988.

**D i a g n o s i s :** as for species.

**D e s c r i p t i o n :** as for species.

**E t y m o l o g y :** The generic name is taken from the trivial name for the type and only species, *protuberosum*, which referred originally to the perceived similarity of the species to the type species of *Prosopon*, *P. tuberosum*. The gender is feminine in honor of GABRIELE WEHNER.

**D i s c u s s i o n :** WEHNER (1988) erected the species *Prosopon protuberosum* based upon two specimens that were (and apparently still are) held in a private collection. Examination of a cast at the BSP, the original description, and illustrations suggests that the species cannot be retained within *Prosopon sensu stricto* based upon the narrow mesogastric region; the large, bulbous ornamentation in the hepatic region; the lack of a well-defined urogastric region; and the much wider frontal area in general in *Protuberosa* as compared to species of *Prosopon*. In addition, the lateral margins of *Protuberosa* are much more sinuous and possess large, spine-like projections not seen in *Prosopon*.

WEHNER (1988) described and illustrated augenrests on the paratype specimen of *Protuberosa protuberosa*. Unfortunately, these features are not visible on the cast of the

holotype available for study at BSP. Comparison of the drawing (WEHNER 1988: text-fig. 7b) and description of the augenrest with those of other species of *Prosopon* suggests that they are quite similar to one another. Both have a swollen, elongate region forming the suborbital margin that protects the eye; in *Prosopon*, this region is the subhepatic region, whereas in *Protuberosa*, it is not clear whether this area corresponds to the subhepatic region based upon the drawing (WEHNER 1988: text-fig. 7b). In addition to those similarities, *Protuberosa* exhibits some similarities to *Prosopon* in possessing well-developed cervical, branchiocardiac, and postcervical grooves and a bi-convex posterior margin. Thus, we place the two genera within the same family.

***Protuberosa protuberosa* (WEHNER, 1988) nov. comb.**

Fig. 2.9

1988 *Prosopon protuberosum* WEHNER, p. 20, pl. 1, figs. 3, 4.

2000 *Prosopon protuberosum* WEHNER – MÜLLER et al., fig. 17B.

**Original description** (translated from WEHNER 1988: 20-21): “Cephalothorax slightly longer than wide (ratio of length to width 1.2), the maximum width falls about in the middle of the branchial region. The outline narrows toward the front, the anterior margin is gently rounded. The anterior carapace region up to the cervical groove appears divided through clearly deposited warts and strong furrows. The part right and left of the mesogastric region is divided by two furrows into three pairs of warts, the furrows between the hepatic, paragastric, and epigastric region are in comparison relatively weak. The individual swellings sharpen toward the lateral margin somewhat, so that the lateral margin from above looks thickly incised and zig-zagged. The mesogastric region bears at its base two rounded swellings, its spine ends only a little before the axially shortly but strongly incised frontal margin. The front margin is curved downward, a distinct rostrum is not recognizable.

In the middle of the carapace the epibranchial region is divided into an inner and outer part through a strong, long furrow between the cervical and branchiocardiac grooves. The outer, swollen part runs likewise sharply toward the lateral margins and terminates the row of incisions of the anterior part. The inner part is fused with a clearly developed epibranchial lobe, but set apart from the urogastric region through a linear indentation.

The cardiac region is in its front part inflated, blister-like, and runs toward the posterior margin in a narrow, rounded spine.

The branchial region, which occupies on the sides perhaps half the length of the cephalothorax, appears to be rounded. It ends in a wide-rimmed, concave posterior margin, which has on both sides of the middle a gentle incision. The second example of the species permits an interesting view of the right side part. This one departs from all other prosopids in having an unusually large gap between the hepatic and subhepatic swellings. Toward the posterior this gap becomes terminated through the outside larger swelling of the epibranchial region. The resulting cavity could serve for the reception of an unusually long eye stalk; the oblong structure of the subhepatic region that is ridge-shaped and with three thick protective spines also speaks for this. The entire carapace surface is uniformly and densely decorated with small warts.”

**Types:** BSP SYL-1, a cast of the holotype which is in a private collection. A paratype is also held in a private collection.

**Discussion:** It is unfortunate that the type material is held in a private collection. Examination of the original type material could lead to a more complete description for the species and therefore the genus.

Family Bucculentidae nov. fam.

**Included genera:** *Bucculentum* nov. gen.

**Diagnosis:** as for genus.

**Discussion:** The massively inflated hepatic regions, augenrest on the hepatic region, and spiny rostrum and frontal margin of the carapace are unique. The augenrest is situated on the hepatic region, such that it is on the dorsal carapace of the animal. Such an arrangement is unique, and highly unusual. In order for the eye to lie in the augenrest, it must extend obliquely posteriorly, an arrangement not usually seen within the Brachyura. In fact, we are unable to find another brachyuran family in which the eyestalk extends in such a manner. This arrangement could be an adaptation to protect the eye, perhaps in this instance from sediment on the bottom or other suspended material that would be associated with the ventral surface of the animal, perhaps related to feeding. It is possible that the massively inflated hepatic region of the carapace is associated with the arrangement of the orbits and augenrest. It appears likely that this region was associated with feeding, either serving as an area for muscle attachments or for a very large digestive gland. It seems probable that the placement of the augenrest was either to place it out of the way of the feeding mechanics of the animal or that the augenrest was displaced as a side effect of the large inflation of the hepatic region of the carapace. In either instance, the combination of characters is unique. In addition to these features, the strongly oblique branchiocardiac groove that nearly intersects the postcervical groove is an unusual feature not seen in other groups.

Genus *Bucculentum* nov. gen.

**Type species:** *Nodoprosopon bucculentum* WEHNER, 1988.

**Other species:** *Bucculentum bachmayeri* nov. spec.

**Diagnosis:** Rostrum projected well beyond frontal margin of carapace, with numerous small spines or three-spined; orbits appearing to be placed under rostrum, augenrest on hepatic region of dorsal carapace, bounded by spines or ridges; frontal margin of carapace may bear spines; hepatic regions strongly inflated and marking widest point on carapace; cervical and branchiocardiac grooves deep; lateral sides of carapace short.

**Etymology:** The genus name was derived from the trivial name, *bucculentum*, Latin for "with full cheeks," obviously a reference to the enormously swollen hepatic regions of the dorsal carapace (WEHNER 1988). The gender is neuter.

**Discussion:** The discovery of the large collection of material collected by BACH-MAYER from the Ernstbrunn quarries indicates that there are two species within the genus. Thus, we are confident that the inflated hepatic regions and oddly placed augen-rests are not teratological but indeed adaptive.

***Bucculentum bucculentum* (WEHNER, 1988) nov. comb.**

Figs. 3.3, 3.4

1988 *Nodoprosopon bucculentum* WEHNER, p. 53, fig. 15, pl. 4, figs. 1, 2, 6.

**Original description** (translated from WEHNER 1988: 54-55): "Carapace longer than wide, whereby the maximum width is measured across the inflated hepatic region, therefore extraordinarily lying in the front region, whereas the sides of the epibranchial and branchial region are almost parallel. The branchial region can thereby be somewhat inflated and narrows toward the ledge-shaped, arched, posterior margin.

The anterior margin carries a well-developed, three-spined rostrum, which by inspection from the front comes to a V-shaped point. Right and left of the base of the rostrum lie a flat, rounded cavity, which serves for the reception of the eyestalk. This cavity becomes protected through three spine-like projections, and indeed from above through the antennal spine, laterally and outside through the anterolateral spine, and from underneath through a fine-toothed suborbital spine. On both sides of the mesogastric region, perhaps at the starting point of the gastric area, lie a clear, large pair of warts [epigastric regions?]. An additional, less clear pair of warts appear further to the lateral margin in an imaginary line with the inner wart pair and the anterolateral spine. Between both these wart pairs progresses a longitudinal furrow from the eye cavity almost to the cervical groove.

The mesogastric region is relatively small, oblique, with two sharp tubercles at the base and a sharp ridge off the gastric extension, on which three successive warts lie.

The epibranchial region is toward the sides narrowed; toward the middle, apart from a small depression in the branchiocardiac groove, smooth, and fused with a small but clear epibranchial lobe. The urogastric region takes in the dorsal line perhaps half the middle part and is therewith relatively large. Small and strikingly formed in comparison is the cardiac region which is clearly inflated. Its outline is distinctly pentagonal, in the middle runs a longitudinal ridge with three warts, of which the last is the largest.

The branchial region can be somewhat inflated, but hardly or not more than the middle part is. It narrows slightly toward the posterior margin, where the carapace ends in a lightly concave posterior margin. The intestinal region is clearly separated from the branchial regions through two short furrows.

The whole carapace is ornamented with small sharp warts."

**Type:** BSP 1980 XXX 1255, holotype.

**Material examined:** In addition to the holotype, casts of BSP 1987 I 55, SMNS 61670/1, and SMNS 61655 were examined.

**Occurrence:** The holotype was collected from the Biburg locality of Oxfordian age in southern Germany (WEHNER 1988).





Fig. 3. Bucculentidae new family. 1, *Bucculentum bachmayeri* new species, holotype, NHMW 1990/0041/3376, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 2, *B. bachmayeri*, paratype, NHMW 2007/0149/0007, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *B. bucculentum*, cast of holotype, BSP 1980 XXX 1255, cataloged as KSU D 602; 4, *B. bucculentum*, actual holotype specimen, Biburg, Germany, Oxfordian (Upper Jurassic). Note differences between cast and holotype and general accuracy of cast. Scale bars = 1 mm.



***Bucculentum bachmayeri* nov. spec.**

Figs. 1.4, 3.1, 3.2

**Diagnosis:** Eyestalk lying transversely across carapace in augenrest bounded by ridge on outer-orbital edge; suborbital margin with two long, attenuated spines directed anterolaterally; distance between outer-augenrest ridges about 78 percent maximum carapace width; urogastric region not well defined, depressed below level of metagastric and cardiac regions; cardiac region small, ovate, raised to prominent sharp point at distal tip.

**Description:** Carapace longer than wide, width about 70 percent maximum length, widest at position of hepatic region, about 35 percent the distance posteriorly on carapace; carapace weakly vaulted longitudinally and moderately vaulted transversely; regions moderately defined by broad grooves.

Rostrum projected well beyond frontal margin of carapace, with triangular tip, lateral margins parallel, ornamented on distal edges with numerous tiny spines; axially sulcate; base of rostrum about 30 percent maximum carapace width. Orbits appearing to have been placed under the rostrum, eyestalk lying transversely across carapace in augenrest on hepatic region bounded by ridge on outer-orbital edge; suborbital margin with two long, attenuated spines directed anterolaterally; distance between outer-augenrest ridges about 78 percent maximum carapace width.

Anterolateral margin markedly convex from swollen hepatic region; remainder of lateral margins nearly parallel to one another, with small constriction at intersection of branchiocardiac groove with lateral margin; segment anterior to branchiocardiac groove weakly convex; segment posterior to intersection of branchiocardiac groove broadly convex; carapace narrowing slightly at posterior end. Posterior margin broadly rimmed, weakly concave, rim widest at lateral edges.

Mesogastric region with long anterior process, widening slightly distally, with one or two tubercles on process and two large tubercles on widened distal portion. Protogastric region narrow, ornamented with several scattered swellings. Metagastric region bilobed, wider than mesogastric, constricted axially on anterior and posterior margins. Urogastric region not well-defined, depressed below level of metagastric and cardiac regions. Cardiac region small, ovate, raised to prominent sharp point at distal tip. Intestinal region elongate-triangular, depressed below level of cardiac region. Hepatic region moderately inflated axially, bearing concavity for eye to rest; strongly inflated laterally, lateral inflation extending well onto lateral sides of carapace and curving posteriorly, bounded posteriorly by ventral extension of cervical groove, ventrally by antennar groove.

Cervical groove sinuous, initially directed obliquely anteriorly, then curving posteriorly around bases of protogastric and mesogastric regions; deepest laterally. Postcervical groove continuous, bounding posterior edge of metagastric region, extending about half the distance laterally, nearly intersecting branchiocardiac groove. Branchiocardiac groove directed strongly obliquely posteriorly, extending in almost straight segments from lateral margin to posterior tip of cardiac region.

Epibranchial region inflated laterally, directed obliquely and essentially parallel to branchiocardiac groove, with flattened area adjacent to cardiac region. Remainder of branchial region broadly inflated.

Carapace surface covered with rimmed pits, especially posteriorly, which when all cuticle layers were present, were probably spines.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Bucculentum bachmayeri* nov. spec. are as follows. L1 = maximum carapace length including rostrum; W1 = maximum carapace width; L2 = length to position of maximum width; W2 = rostral width; W3 = width between outer-augenrest ridges. NHMW/2007/0149/0007, L1 = 15.2, W1 = 10.6, W2 = 3.6, W3 = 8.2, L2 = 6.0; NHMW 1990/0041/3376, L1 = 9.3, W1 = 6.3, W2 = 1.8, W3 = 5.1, L2 = 3.2; NHMW 1990/0041/3371, L1 = >9.4, W1 = 8.0, W3 = 6.2; NHMW 1990/0041/1511, L1 = 5.4, W1 = 4.0, W3 = 3.0, L2 = 2.1.

**Etymology:** The trivial name honors FRIEDRICH BACHMAYER, late of the Vienna Museum, who collected the vast quantities of fossil decapod material from the Ernstbrunn quarries, therefore making a massive contribution to the study of Jurassic decapod crustaceans.

**Types:** The holotype, NHMW 1990/0041/3376, and three paratypes, NHMW 1990/0041/1511, NHMW 1990/0041/3371, and NHMW/2007/0149/0007.

**Occurrence:** The specimens were collected from the Ernstbrunn quarry localities.

**Discussion:** The new species differs from the type species in the type of ornamentation of the orbital area as well as in the overall proportions of the carapace. *Bucculentum bucculentum* possesses three spines surrounding the augenrest on the hepatic region, whereas *B. bachmayeri* has an outer-augenrest ridge and two suborbital spines that are not present on *B. bucculentum*. In addition, *B. bachmayeri* shows tiny, yet obvious, spines on the rostrum that are not seen in *B. bucculentum*. *Bucculentum bachmayeri* is overall longer and less antero-posteriorly compressed than is *B. bachmayeri*.

#### Superfamily Glaessneropssoidea PATRULIUS, 1959

**Included families:** Glaessneropsidae PATRULIUS, 1959; Lecythocaridae nov. fam.; Longodromitidae nov. fam.; Nodoprosopidae nov. fam.

**Diagnosis:** Carapace longer than wide or wider than long, regions generally well defined by grooves; carapace ornament often well developed, may be composed of tubercles, small spines, large spines, or large swellings; rostrum projecting well beyond orbits, axially sulcate, inflated, or trilobed; orbits well developed; orbit usually ornamented with supra- and sub-orbital spines, fronto-orbital width always occupying entire frontal margin of carapace; augenrest absent; cervical and branchiocardiac grooves usually equally developed, postcervical groove usually present; subhepatic swelling usually present; branchial regions often very short in lateral view; cardiac region always well marked, variable in size.

**Discussion:** Several Jurassic brachyurans can be characterized by possession of well-developed orbits and lack of an augenrest. These same taxa are generally well ornamented, with deep grooves, and with large, projected rostra. These features unite these otherwise rather diverse genera, which we herein array into four families, three of which are new, and one of which is newly elevated, into one superfamily. Because

the orbital, rostral, and overall dorsal carapace structure has heretofore been overlooked, in part because of a lack of well-preserved material, we are able to subdivide these organisms in a way that unites them based upon similarities and recognizes obvious differences between them.

#### Family Glaessneropsidae PATRULIUS, 1959

Included genera: *Glaessneropsis* PATRULIUS, 1959; *Verrucarcinus* nov. gen.

**Diagnosis:** Carapace longer than wide, widest at position of epibranchial or branchial region, about half to three-quarters the distance posteriorly on carapace; carapace regions flattened or bulbous, may be ornamented with large granules, especially large on branchial regions. Rostrum projected well in advance of orbits, spatulate, downturned, with longitudinal swellings and sometimes axial sulcus, tip of rostrum may have spines, rostral width usually about half maximum carapace width but rarely as narrow as one-third carapace width. Eyestalk arising beneath rostrum. Orbit bounded on inner angle by rostrum; upper orbital margin with intra-orbital spine that may be rectangular or triangular in shape; intra-orbital spine may be bounded by deep fissures; fissures and spine directed forward or anterolaterally; outer-orbital angle formed of long, triangular, forward-directed spine that wraps around laterally into cup-shaped structure; orbit directed forward; fronto-orbital width 75-95 percent maximum carapace width. Metagastric region bilobed when well marked. Cervical and branchiocardiac grooves usually well-developed but rarely may be shallow and discontinuous; cervical groove originating at lateral margin just posterior to position of outer-orbital spine; postcervical groove usually present, when present continuous and crossing axis to bound anterior edge of cardiac region. Cardiac region usually small, positioned well anterior of posterior margin but rarely extending toward posterior margin. Subhepatic region markedly inflated, bounded posteriorly by ventral extension of cervical groove, ventrally by antennar groove; anterior margin forms orbital margin. Epibranchial region extending onto lateral side, bounded by ventral extensions of cervical and branchiocardiac grooves.

**Discussion:** The spatulate front with longitudinal swellings; forward-directed orbits; and well-developed orbital components is unique among the Brachyura. In addition, members of the family possess a distinct cervical groove that always originates just posterior to the outer-orbital spine. The orbital ornamentation is in some ways reminiscent of majoid crabs; however, none of the remainder of the features of the carapace can place these crabs within any existing families within the Majoidea SAMUELLE, 1819. The Glaessneropsidae is easily differentiated from the Longodromitidae nov. fam., in which the cervical groove originates well posteriorly on the carapace from the outerorbital spine and extends nearly straight across the carapace. Both the Longodromitidae and the Lecythocaridae nov. fam. have well-differentiated axial regions of the carapace and branchial regions that are not seen in members of the Glaessneropsidae. Members of the Nodoprosopidae nov. fam. have a unique rostrum with three attenuated spines and no evidence of any orbital structures, as well as differentiated axial region, setting members of that family apart from the other three discussed here. Thus, each family is distinctive.

Genus *Glaessneropsis* PATRULIUS, 1959

Type species: *Prosopon heraldicum* MOERICKE, 1897, by original designation.

Included species: *Glaessneropsis bucegiana* PATRULIUS, 1959; *G. heraldica* (MOERICKE, 1897); *G. myrmekia* nov. spec.; *G. tribulosa* nov. spec.

Note: PATRULIUS (1959) apparently intended that *Glaessneropsis* be feminine in gender, based upon his use of the combinations *Glaessneropsis heraldica* and *Glaessneropsis bucegiana* in his (1959) paper.

Diagnosis: Carapace longer than wide; lateral sides short, weak crest and granules separating dorsal and lateral sides of carapace; rostrum extending well beyond orbits, spatulate, downturned distally, widened at base; axially sulcate, with keels parallel to sulcus; orbits directed forward, with intra-orbital, outer-orbital, and sub-orbital spines, orbital spines directed forward; cervical and branchiocardiac always present, postcervical groove usually present; cervical groove originating just posterior to orbits, extending axially; regions generally poorly to moderately developed; cardiac region spherical or elongate; subhepatic region inflated.

Discussion: Examination of material collected from the Ernstbrunn quarry localities and the Štramberk locality indicate that *Glaessneropsis* is a relatively speciose genus, especially for the Jurassic. There is broad variability within the genus with respect to the development of the cervical groove, which can be deep or shallow, concave forward or relatively straight, and complete or discontinuous. Members of the genus may possess a deep postcervical groove or lack one altogether. However, all are united by the distinctive rostrum and orbital configuration, which is unique among Brachyura of any age.

*Glaessneropsis heraldica* (MOERICKE, 1897)

Figs. 4.1-4.3

- 1897 *Prosopon heraldicum* MOERICKE, p. 58, pl. 6, fig. 13.
- 1959 *Glaessneropsis heraldica* – PATRULIUS, p. 254.
- 1988 *Glaessneropsis heraldica* (MOERICKE, 1889 [error pro 1897]) – WEHNER, p. 116, pl. 8, fig. 1.
- 2000 *Glaessneropsis heraldica* (MOERICKE, 1889 [error pro 1897]) – MÜLLER et al., p. 55, figs. 16, 18H.

Diagnosis: Carapace longer than wide; cervical groove deep, concave anteriorly; branchiocardiac groove and postcervical grooves deep; carapace widest at epibranchial regions, about half the distance posteriorly.

Description: Carapace longer than wide, width about 60 percent maximum carapace length; moderately inflated transversely and longitudinally; lateral sides short, weak crest and granules separating dorsal and lateral sides; regions marked by deep transverse grooves and moderate swellings.

Rostrum extending well beyond orbits, markedly downturned distally, spatulate, with rounded tip; axially sulcate; sulcus bounded by two longitudinal ridges; lateral margins of rostrum sinuous, widened distally; with widened, rounded projection at base serving as inner orbital angle.



Fig. 4. *Glaessneropsis* spp. 1, *Glaessneropsis heraldica*, cast of holotype, BSP AS III 306, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 2, *G. heraldica*, NHMW 1990/0041/278, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *G. heraldica*, NHMW 1990/0041/277, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 4, *Glaessneropsis myrmekia* new species, NMHW 2007z0162/0003, holotype, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 5, *Glaessneropsis tribulosa* new species, NHMW 1990/0041/272, holotype, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 6, *G. tribulosa*, NHMW 1990/0041/3115, paratype, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 7, *G. tribulosa*, NHMW 1990/0041/271, paratype, oblique anterior view showing orbit, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars = 1 mm.



Orbit consisting of opening under rostrum from which eyestalk emerges, cup-shaped orbit facing forward, directed forward; deep; with large intra-orbital spine and outer-orbital spines, spines directed forward; suborbital margin apparently with spine; fronto-orbital width about 80-85 percent maximum carapace width. Carapace widest at epibranchial region, lateral margins convex overall, constricted where intersected by cervical and branchiocardiac grooves. Posterior margin rimmed.

Mesogastric region triangular, faintly marked, widening posteriorly. Protogastric region broad, flattened. Hepatic region tiny, circular, situated along lateral margin just posterior to orbit. Cervical groove very deep, concave forward. Mesogastric and epibranchial regions not differentiated, bounded anteriorly by deep cervical groove and posteriorly by deep branchiocardiac groove and postcervical groove. Branchiocardiac groove deep, parallel to cervical groove until reaching cardiac region, where it becomes much shallower and curves posteriorly to bound cardiac region.

Postcervical groove deep, intersecting branchiocardiac groove on left and right side of cardiac region, bounding anterior edge of cardiac region and joining with arcs of branchiocardiac groove to make a convex-forward groove paralleling cervical groove.

Branchial regions undifferentiated, ornamented with tubercles. Cardiac region weakly inflated anteriorly, parallel sided, rounded posteriorly.

Subhepatic region inflated, bounded posteriorly by ventral extension of cervical groove and ventrally by antennar groove. Subepibranchial region moderately inflated, bounded by ventral extension of branchiocardiac groove on posterior and ventral margins.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Glaessneropsis heraldica* are presented in Table 4.

Table 4. Measurements (in mm) taken on the dorsal carapace of species of *Glaessneropsis* spp. L1 = maximum carapace length; W1 = maximum carapace width; W2 = rostral width; W3 = fronto-orbital width; L2 = length to maximum width.

Specimen number	L1	W1	W3	W2	L2
<i>Glaessneropsis heraldica</i>					
Cast of holotype, BSP AS III 306	5.5	3.6	2.9	1.2	2.6
NHMW 1990/0041/277	5.6	3.3	5.8	1.2	2.6
NHMW 1990/0041/278					
<i>Glaessneropsis tribulosa</i> new species					
NHMW 1990/0041/4772	5.6	4.0	3.3	1.6	3.2
NHMW 1990/0041/272 (holotype)	4.1	3.1	2.9	1.4	2.6
NHMW 1990/0041/271	5.5	3.8	3.0	1.8	3.7
NHMW 1990/0041/3115	3.2	2.2	2.0	1.0	1.6
<i>Glaessneropsis myrmekia</i> new species					
NHMW 2007z0162/0003 (holotype)	5.5	3.6	2.9	1.2	2.6

**Material examined:** The original specimen of MOERICKE (1897), interpreted to be the holotype, BSP AS III 306; and NHMW 1990/0041/277 and NHMW 1990/0041/278.



**Occurrence:** The holotype was collected from the Štramberg locality, and the NHMW specimens were collected from the Ernstbrunn quarry localities.

**Discussion:** The new material makes it possible to provide a more complete description for the type species of the genus. We refer the two Ernstbrunn specimens to *Glaessneropsis heraldica* based upon their possession of deep, parallel cervical and branchiocardiac grooves which are seen in the type specimen, as well as the strong rostrum that is weakly downturned. The carapace of the Ernstbrunn specimens is markedly longer than wide as in the type specimen. The Ernstbrunn specimens appear to have a somewhat larger and better-developed rostrum than does the type specimen; however, the rostrum of the type is not fully prepared from the surrounding matrix. Thus, we refer them to *G. heraldica* rather than naming a third new species.

***Glaessneropsis tribulosa* nov. spec.**

Figs. 4.5-4.7

**Diagnosis:** Rostrum with tiny spines on tip; cervical and branchiocardiac grooves very weak; postcervical groove absent; branchial margins with tiny spines.

**Description:** Carapace longer than wide, width about 70-75 percent maximum carapace width, position of maximum width about two-thirds the distance posteriorly at about mid-branchial region; carapace moderately vaulted transversely and flattened longitudinally except for rostrum, which is strongly downturned distally; regions poorly marked by shallow grooves, flattened.

Rostrum projected well beyond orbits, spatulate, with rounded tip, shallowly axially sulcate, with weak keels parallel to sulcus; with tiny spines on entire distal edge; widened at base, forming inner orbital angle.

Orbits arising from under rostrum, eye lying in deep concavity, directed forward; intra-orbital spine short, directed forward; outer-orbital spine short, triangular, directed forward; suborbital spine triangular, directed forward; fronto-orbital width ranging from 80 to 95 percent maximum carapace width. Lateral margins weakly convex, weakly constricted where intersected by cervical and branchiocardiac grooves. Posterior margin nearly straight. Branchial and posterior margins with tiny, triangular spines.

Rostrum separated from dorsal carapace regions by transverse furrow. Mesogastric region narrow, triangular, best marked posteriorly, with weak axial longitudinal keel. Protogastric and hepatic regions not differentiated, narrowing laterally. Cervical groove shallow to almost unmarked laterally, extending in straight segment toward axis, then extending in more posteriorly directed, deeper, straight segment bounding posterior margin of mesogastric region. Metagastric and epibranchial regions poorly differentiated. Branchiocardiac groove sinuous laterally, deepening as it approaches cardiac region, weakly diverging posteriorly to bound cardiac region. Postcervical groove absent. Cardiac region very weakly developed, spherical. Branchial regions undifferentiated, flattened.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Glaessneropsis tribulosa* nov. spec. are presented in Table 4.

**E t y m o l o g y :** The trivial name is derived from the Latin word *tribulosus*, meaning thorny, in reference to the tiny spines on the rostrum and lateral margins of the branchial regions of the carapace.

**T y p e s :** The holotype, NHMW 1990/0041/272, and paratypes NHMW 1990/0041/271, NHMW 1990/0041/3115, NHMW 1990/0041/4772.

**O c c u r r e n c e :** All of the specimens were collected from the Ernstbrunn quarry localities.

**D i s c u s s i o n :** *Glaessneropsis tribulosa* nov. spec. is easily differentiated from *Glaessneropsis heraldica* by its poorly developed cervical and branchiocardiac grooves and lack of a postcervical groove. The presence of two species of the same genus is quite common in Jurassic rocks. Because there are no preserved sterna or abdomina for these crabs, it is not possible to test whether or not these multiple forms represent sexual dimorphs. The most common expression of secondary sexual characters is in the size of the chelipeds and chelae, which are larger in males. Unfortunately, the chelae are not found associated with the dorsal carapace in Jurassic brachyurans. However, it is important to note that brachyurans typically do not exhibit secondary sexually dimorphic characters of the dorsal carapace, and where they do, it is in the form of larger or smaller anterolateral spines or other minor ornamentation (FELDMANN & SCHWEITZER 2007), not in major aspects of the carapace such as development of groove patterns. Thus, the different forms described herein are most likely different species.

### ***Glaessneropsis myrmekia* nov. spec.**

Fig. 4.4

**D i a g n o s i s :** Carapace much longer than wide; regions well developed, inflated, and ornamented with granules; cardiac region longer than wide; rostrum with tip that is perpendicular to dorsal carapace.

**D e s c r i p t i o n :** Carapace longer than wide, width about 60 percent maximum length, widest at mid-branchial region about 70 percent the distance posteriorly, carapace widening noticeably posteriorly; carapace markedly vaulted transversely and longitudinally; regions well marked by grooves, inflations, and ornamentation.

Rostrum extending well beyond orbits, strongly downturned distally so that tip is oriented at almost 90 degree angle to rest of carapace; deeply axially sulcate, with strong keels parallel to axial sulcus, with blunt tip, widened at base to form inner-orbital angle.

Orbits directed forward; intra-orbital spine stout, directed anterolaterally; outer-orbital spine with broad base, becoming attenuated distally, arcuate, directed anterolaterally; fronto-orbital width about 85 percent maximum carapace width. Lateral margins of carapace sinuous, constricted where intersected by cervical and branchiocardiac grooves, bulbous between constrictions, ornamented with small spines along lateral margin of branchial regions. Posterior margin broadly rimmed, weakly concave axially.

Rostrum separated from dorsal carapace regions by deep, transverse furrow. Mesogastric region triangular, widest posteriorly, with large tubercle on anterior projection and transverse swelling posteriorly. Protogastric and hepatic region not differentiated, with

three large swellings. Metagastric region bilobed, granular, axially constricted. Epibranchial regions spherical, lateral to mesogastric region, granular.

Cervical groove deep, concave forward, extending from just posterior to outer-orbital spine to bound posterior margin of mesogastric region. Branchiocardiac groove deep, extending in almost straight path posteriorly and axially to cardiac region, then diverging posteriorly to bound cardiac region. Postcervical groove convex forward, bounding anterior margin of cardiac region, intersecting branchiocardiac groove on left and right side of cardiac region. Cardiac region much longer than wide, initially straight, then converging posteriorly to sharp point, granular. Branchial region largely undifferentiated, moderately inflated, with large granules overall.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Glaessneropsis myrmekia* nov. spec. are presented in Table 4.

**Etymology:** The trivial name is derived from the Greek word *myrmekia*, meaning wart, in reference to the granular ornamentation on the entire dorsal carapace of the species, unusual within the genus.

**Type:** The holotype and sole specimen is NHMW 2007z0162/0003.

**Occurrence:** The specimen was collected from the Štramperk locality.

**Discussion:** *Glaessneropsis myrmekia* nov. spec. is easily differentiated from all other species of *Glaessneropsis* in possessing highly ornamented regions; a rostral tip that is perpendicular to the rest of the dorsal carapace; and a large cardiac region that is longer than wide. No other species within the genus have any of these features, let alone a combination of these characters.

#### Genus *Verrucarcinus* nov. gen.

*Prosopon* VON MEYER (part).

*Nodoprosopon* BEURLIN, 1928 (part).

**Type species:** *Prosopon torosum* VON MEYER, 1857.

**Included species:** *Verrucarcinus ordinatus* (COLLINS in COLLINS & WIERZBOWSKI, 1985), as *Nodoprosopon*; *V. torosus*.

**Diagnosis:** Carapace longer than wide, widest at position of branchial regions, about three-quarters the distance posteriorly on carapace; carapace regions bulbous, ornamented with large granules, especially large on branchial regions. Rostrum projected well in advance of orbits, spatulate, downturned, with triangular axial swelling, flattened on either side of swelling, tip of rostrum with spines, rostral width about half maximum carapace width. Eyestalk appearing to have arisen beneath rostrum. Orbit bounded on inner angle by rostrum; upper orbital margin formed of rectangular intra-orbital spine bounded by deep, open fissures; fissures and spine directed anterolaterally; outer-orbital angle formed of spine with long, triangular, forward-directed spine that wraps around laterally into cup-shaped structure; orbit directed forward; fronto-orbital width about 75 percent maximum carapace width. Metagastric region bilobed; cervical and branchiocardiac grooves well developed; postcervical groove absent. Cardiac region small, circular, positioned well anterior of posterior margin.

**Etymology:** The generic name is derived from the Latin word *verrucosus* meaning full of warts and the Greek word *karkinos*, meaning crab, the Latinized version of which is a common stem used within the order. It refers to the large number of swellings on the dorsal carapace. The gender is masculine.

**Material examined:** *Nodoprosopon beurleni* KUHN, 1936, holotype BSP 1931 XI 70; *Nodoprosopon ordinatum* COLLINS in COLLINS & WIERZBOWSKI, 1985, holotype, IGPUW/C/1/6.

**Discussion:** The unique orbits in this taxon clearly warrant the naming of a new genus to accommodate it. The combination of well-developed orbital structures; well-developed cervical, branchiocardiac, and postcervical grooves; and a spatulate rostrum with a triangular axial swelling are unique in the Brachyura. *Verrucarcinus* is easily differentiated from *Glaessneropsis*, the other genus within the family, by differences in the rostral structure.

WEHNER (1988) considered *Prosopon torosum* as a species of *Nodoprosopon* and synonymized *Nodoprosopon beurleni* KUHN, 1936 with it. Examination of the holotype of *N. beurleni* suggests that this is an appropriate synonymy, because the holotype of *N. beurleni* possesses all of the diagnostic features of the dorsal carapace of *Verrucarcinus torosus*. She also synonymized *Nodoprosopon ordinatum* COLLINS in COLLINS & WIERZBOWSKI (1985) with *N. torosum*. However, examination of the holotype of *N. ordinatum* (Fig. 5.3) demonstrates that it differs from *V. torosus* in possessing a more narrow metagastric region, a narrower rostrum, a shorter intra-orbital spine, and spherical inflations to either side of the cardiac region. Because *N. ordinatum* possesses the orbital structure diagnostic for *Verrucarcinus* as well as the bilobate metagastric region and small, spherical cardiac region that is positioned well anterior to the posterior margin and lacks a postcervical groove, we place it within *Verrucarcinus*. Thus, two species of the genus are known, each from the Jurassic. *Verrucarcinus ordinatus* was collected from Oxfordian rocks in Poland and was well described and illustrated previously (COLLINS & WIERZBOWSKI 1985; SCHWEITZER et al. 2007: fig. 2.9 non fig. 2. 6).

***Verrucarcinus torosus* (VON MEYER, 1857) nov. comb.**

Figs. 1.5, 5.1, 5.2, 5.4, 5.5

- 1857 *Prosopon torosum* VON MEYER, p. 556.
- 1860 *Prosopon torosum* – VON MEYER, p. 214, pl. 23, fig. 30;
- 1924 [imprint 1925] *Prosopon torosum*, VON MEYER – VAN STRAELEN, p. 372.
- 1925 *Prosopon torosum* H. V. MEYER – BEURLIN, p. 486.
- 1928 *Nodoprosopon torosum* (VON MEYER, 1857) – BEURLIN, p. 147.
- 1929 *N. torosum* (V. MEYER) – GLAESSNER, p. 273.
- 1933 *N. torosum* (V. MEY.) – GLAESSNER, p. 180.
- 1936 *Nodoprosopon beurleni* KUHN, p. 120, fig. 1.
- 1985 *Nodoprosopon torosum* (VON MEYER, 1857 [error pro 1859]) – COLLINS in COLLINS & WIERZBOWSKI, p. 80, pl. 1, fig. 7.
- 1988 *Nodoprosopon torosum* (VON MEYER, 1857 [error pro 1859]) – WEHNER, p. 50, pl. 3, figs. 6-9
- 2000 *Nodoprosopon torosum* (VON MEYER, 1857 [error pro 1859]) – MÜLLER et al., fig. 17H.
- 2007 *Prosopon torosum* V. MEYER – SCHWEITZER et al., p. 103, fig. 2.10.

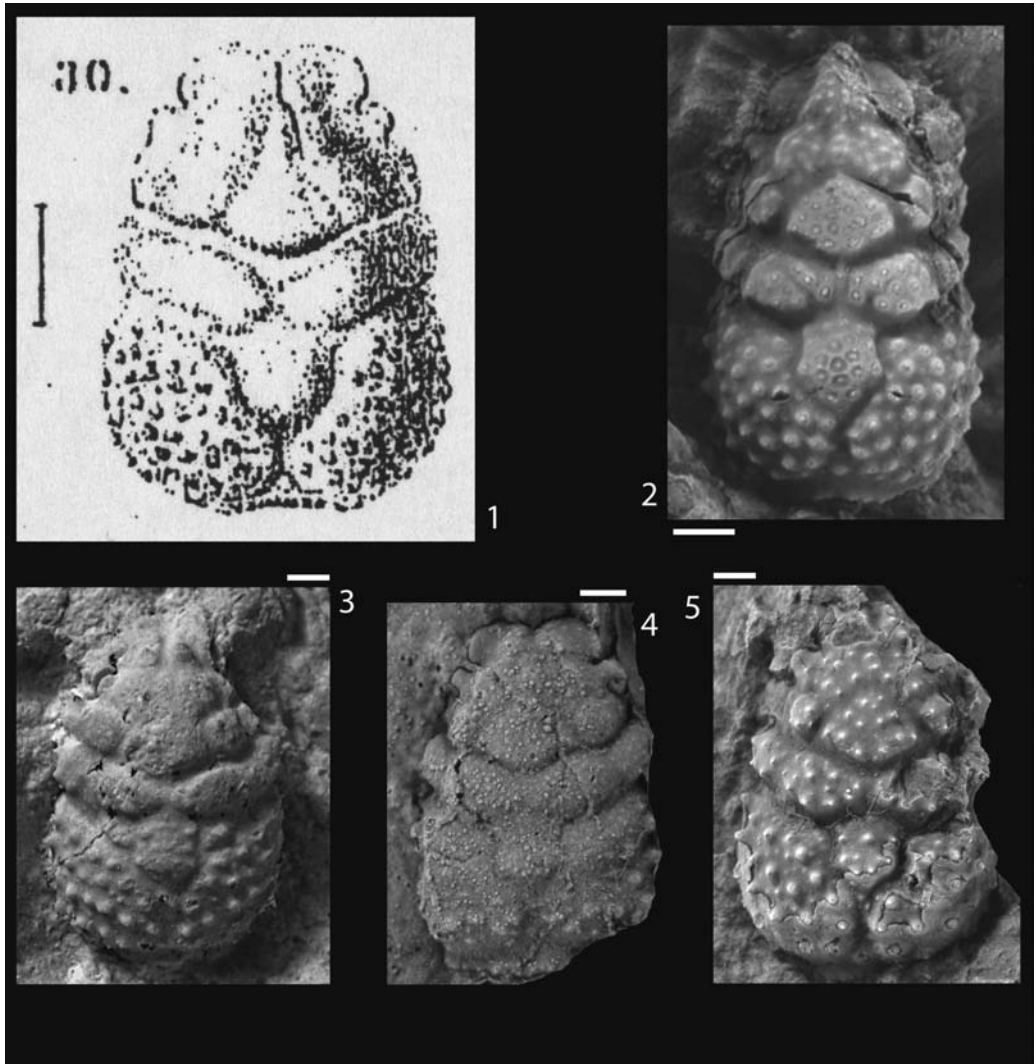


Fig. 5. *Verrucarcinus* spp. 1, *Verrucarcinus torosus*, digital image from VON MEYER (1860: pl. 23, fig. 30); 2, *V. torosus*, NHMW 1990/0041/3476 with well-preserved rostrum and orbits, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *V. ordinatus*, holotype IGPUW/C/1/6, Podzamcze at Zawiercie, Polish Jura, Oxfordian (Upper Jurassic) (COLLINS and WIERZBOWSKI, 1985); 4, *V. torosus*, neotype, BSP 1881 IX 686, Oerlinger Tal, Germany, Upper Jurassic; 5, *V. torosus*, SMNS 61674, Eichen, Weiss Jura delta. Scale bars = 1 mm. Scale bar in VON MEYER illustration is of unknown length.



**Original description** (translated from VON MEYER 1860: 214): “The smallest cephalothorax among five of these specimens investigated is complete and well preserved, 0.0065 long and 0.0045 (units for these measurements unknown) in maximum width, which lies in the posterior half of the branchial region. From here the cephalothorax narrows gradually toward the front. According to the largest example, the cephalothorax attains a width of 0.0075. In this example on account of the absence of the front half, the length is not known. In the illustrated cephalothorax, the smallest, the length of the anterior part measured in the posterior part not entirely half the complete length [we are unsure what was meant here]. The gastric region is clearly distinct, most sharply at the hind end of the outside and near to a spine, which ends some distance from the front end of the cephalothorax. This end is like that in *Prosopon paradoxum*, only it is shorter. The narrow, deep incision in the region of the outer edges corresponding to the front end of the gastric region is present. The tubercle of the hepatic region is too weakly developed for an exact description. The transverse furrow of the genital region is in the posterior retracted and weakly separated. The cardiac region is about equal in length and width and similarly formed as in *Prosopon spinosum* and *P. excisum*. The swelling directed toward the cardiac region, which in both these latter species is well developed, is missing completely. The length of the branchial region attains on the outside almost half the length of the cephalothorax. It is decorated with strong warts, which is all the more striking, because the whole remaining cephalothorax appears smooth and only under the hand lens are detected weak indications of uniform tubercles. The hind end of the cephalothorax is hardly indented, sometimes however with a sharp rim, whose hind margin is decorated with warts.”

**Type**: WEHNER (1988) designated a neotype, BSP 1881 IX 686. In her remarks, she considered that the specimen may have been one of the original specimens that VON MEYER described in 1860, based upon a handwritten note associated with the specimen and its remarkable similarity to VON MEYER’s 1860 illustration (WEHNER 1988: 51). Indeed, the specimen number, which contains “1881,” indicates that it is from an old collection (M. NOSE, personal communication, July, 2006) and therefore could indeed be a VON MEYER original. In any case, the neotype agrees well with the 1860 description and illustrations.

**Description of neotype and other material**: Carapace about two-thirds to three-quarters as wide as long, widest in branchial region about 78 percent the distance posteriorly; moderately vaulted transversely and longitudinally; carapace regions bulbous, ornamented with large granules, especially large on branchial regions.

Rostrum projected well in advance of orbits, spatulate, downturned, with triangular axial swelling, flattened on either side of swelling, tip of rostrum with spines, rostral width about half maximum carapace width. Eyestalk appearing to have arisen beneath rostrum. Orbit bounded on inner angle by rostrum; upper orbital margin formed of rectangular projection bounded by deep, open fissures; fissures and projection directed anterolaterally; outer-orbital angle formed of long, triangular, forward-directed spine that wraps around laterally into cup-shaped structure; orbit itself directed forward; fronto-orbital width about 75 percent maximum carapace width.

Lateral margins of carapace well ornamented. Segment anterior to intersection of cervical groove keeled; segment between cervical and branchiocardiac grooves with two

nodes; segment posterior to branchiocardiac groove ornamented with numerous large granules. Posterior margin broadly rimmed, nearly straight.

Protogastric region broad, ornamented with smaller tubercles; with an isolated, larger swelling positioned lateral to base of mesogastric region; hepatic region circular, just posterior to orbit; mesogastric region broadly triangular, terminating well before rostrum; metagastric region wide, axially constricted, posteriorly appearing bilobed; urogastric region a broad, deep depression; cardiac region pentagonal, ornamented with scattered granules; intestinal region triangular, directed toward cardiac region, depressed well below level of branchial regions.

Cervical groove deep, composed of three broadly concave-forward arcs bounding protogastric and mesogastric regions, overall path concave forward. Branchiocardiac groove parallel to cervical groove and somewhat deeper, becoming weaker as it bounds cardiac region. Epibranchial regions rounded, situated lateral to metagastric region, well separated from metagastric by deep groove. Remainder of branchial region undifferentiated, broadly inflated, ornamented with large tubercles.

Subhepatic region moderately inflated, bounded posteriorly by ventral extension of cervical groove which is directed posteroventrally. Epibranchial region extending onto lateral side, bounded by ventral extensions of cervical and branchiocardiac grooves.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Verrucarcinus torosus* are found in Table 5.

Table 5. Measurements (in mm) taken on the dorsal carapace of specimens of *Verrucarcinus torosus*. L1 = maximum carapace length; W1 = maximum carapace width; L2 = length to position of maximum width; W2 = rostral width; W3 = fronto-orbital width. \* holotype of *Nodoprosopon beurleni*. Remainder of specimens originally referred to *Prosopon torosum* or *Nodoprosopon torosum* on labels.

Specimen Number	L1	W1	W2	W3	L2
BSP1881 IX 686	7.7	5.2	2.8	4.6	5.9
SMNS 67178	-	11.8	-	8.6	-
SMNS 61674	9.7	7.1	-	-	7.9
SMNS 61631a	13.9	9.3	5.2	7.2	10.6
VON MEYER (1860: pl. 23, fig. 30)	24	18	9	15	19
BSP1931 XI 70*	16.4	10.7	-	-	12.5

**Material examined:** Neotype of *Prosopon torosum*, BSP 1881 IX 686; specimens labeled as *Nodoprosopon torosum*, SMNS 61631a, SMNS 61674, SMNS 67178; holotype of *Nodoprosopon beurleni*, BSP 1931 XI 70; NHMW 1990/0041/3476.

**Discussion:** *Verrucarcinus torosus* has been variously referred to *Prosopon* and *Nodoprosopon* over the past 150 years. In more recent works, it has been considered as *Nodoprosopon* except by SCHWEITZER et al. (2007), who severely restricted the diagnosis of *Nodoprosopon* and referred the species back to *Prosopon sensu lato*.

Family *Lecythocaridae* nov. fam.

Included genus: *Lecythocaris* VON MEYER, 1860.

**Diagnosis:** Generally small crabs, triangular in outline, with widest part in metabranchial region which is extremely large and bears a prominent node or swelling on anterolateral corner; regions strongly inflated and separated by distinct, deep grooves; grooves not necessarily identifiable as cervical, branchiocardiac, and postcervical. Rostrum broad, spatulate, axially sulcate, and strongly downturned. Orbits circular, rimmed, separated from rostrum by prominent, open notch; with inner suborbital spine. Mesogastric region narrow. Cardiac region very large, extending nearly to posterior border and completely separating metabranchial regions. Hepatic and epibranchial regions developed as globose swellings.

**Discussion:** The combination of characters defining the new family clearly distinguish the genus *Lecythocaris* and, therefore, the family from other genera that previously have been assigned to the Prosopidae VON MEYER, 1860. The lack of augenrests places it within the Glaessneropsoidea, but the complex groove pattern and orbital ornamentation that differs from other members of the superfamily require a new family to embrace it. The enormously globular swellings of the dorsal carapace and the large cardiac region that extends to the posterior margin of the carapace are not seen in any other brachyurans.

Genus *Lecythocaris* VON MEYER, 1860

Type species: *Prosopon paradoxum* VON MEYER, 1858.

Included species: *Lecythocaris obesa* nov. spec.; *L. paradoxa* (VON MEYER, 1858).

**Diagnosis:** As for family.

**Discussion:** There seems to be some confusion about the date of naming of the type species. Although denoted in the Treatise as having been named in 1860 (GLAESSNER 1969), GLAESSNER (1929) indicated that the species was named and referred to *Prosopon* by VON MEYER in 1858. The 1858 timing of the naming is confirmed by examination of the original brief notice (VON MEYER 1858: 61) as well as by the citation of VON MEYER (1860: 215).

Recognition of a second species of the genus makes it possible to define the characters that distinguish the genus more succinctly. The architecture of the orbital region and the generally globose nature of the regions and projections from regions, coupled with the general outline of the carapace, readily distinguish members of this genus from other Jurassic forms. Another point of distinction is that the cardiac region is very large and extends almost to the posterior margin, clearly separating the metabranchial regions. The branchiocardiac groove is well developed around the cardiac region, almost intersects the posterior rim of the carapace, and becomes interrupted as it passes between the epibranchial and mesobranchial regions.

It is tempting to draw a comparison between the form of *Lecythocaris* and that of modern majoids and parthenopoids. The triangular outline and development of bulbous regions is quite reminiscent of these extant forms. In fact, PATRULIUS (1959: 253)

noted that *L. paradoxa* might be the progenitor of the Oxyrhyncha, the traditional group to which the majoids and parthenopoids were assigned. However, the similarity is superficial because the form of the rostrum and the details of construction of the orbits is quite different. The rostrum of majoids tends to be narrow and strongly bifid and that of the parthenopoids is very small. The orbits of parthenopoids are tiny and those of the majoids tend to be complexly constructed of eaves, spines, and the basal segment of the antennae. Generally, the orbits of majoids are not directed forward. The orbits of *Lecythocaris* spp. are circular, forward-directed, and separated from the rostrum by a deep, open fissure. The orbital rim is simple. Thus, it is far more likely that the form of the species of Lecythocaridae is analogous to that of the majoids and may be an adaptation to a semi-cryptic, benthic lifestyle in which concealment in vegetation or niches within a firm substrate was facilitated by a compact body form and irregular outline.

***Lecythocaris paradoxa* (VON MEYER, 1858)**

Figs. 6.1-6.5

**Diagnosis:** Carapace small, triangular, with greatest width in posterior one-third. Anterior process of metagastric region with keel and node. Protogastric region with a large, pointed node and cardiac region with three nodes. Metabranial region with large spine on anterolateral corner.

**Description** (translated from VON MEYER 1860: 215-216): "The cephalothorax of this species is so strikingly formed that one can scarcely be led to believe that it can be classified as a Prosopidae. Four correspondingly shaped examples exist. A typical difference from *Prosopon* does not exist, the discrepancy depends only on dividing them by grade of evolution and expansion of the individual parts. The cephalothorax is barely 0.006 long and slightly more than 0.005 wide (units for these measurements unknown). The greatest width occurs in the posterior half and is caused by the inflated branchial region. The anterior half of the cephalothorax narrows anteriorly, and the front quarter is shaped broad and tongue-like. The front comprises little more than half the length. The gastric region is scarcely half the length of the frontal region and in other respects is noticeably narrow. The posterior bears two or three small tubercles. A shallow groove is formed on the front of the hepatic region and is not incised at the front end. With the inception of the broad tongue-shaped division, the outer edge presents itself as distinctly incised. Behind it in each half of the hepatic region are situated three pustules near each other, which are conspicuous in size, and which follow the oblique position of the anterior transverse groove [cervical groove]. Of these pustules the one placed nearest the gastric region is sharpest. The posterior transverse furrow [branchiocardiac groove] is almost more distinctly developed than the anterior one. The outer part of the genital region [urogastric region] consists on each side of two pustules lying next to one another which are even stronger than the hepatic region. The posterior transverse band [branchiocardiac groove] is narrow and has a pair of transversely oval mounds placed within it; which from the outer side of the urogastric region are more deeply separated than from the gastric and cardiac regions. The cardiac region is rounded rhombic-shaped, noticeably large, strongly developed, and commonly with

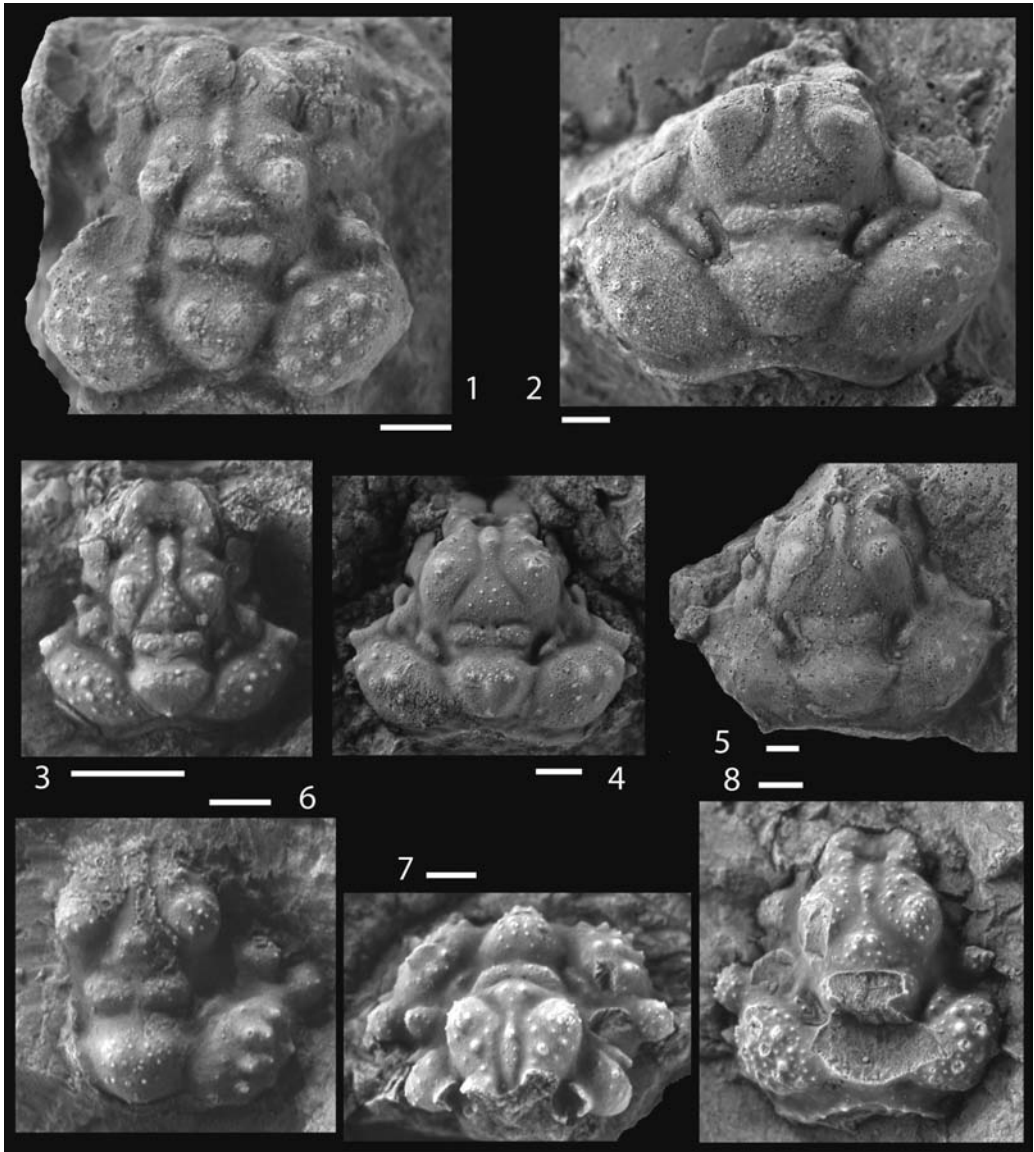


Fig. 6. Lecythocaridae new family. 1, *Lecythocaris paradoxa*, neotype, Museum Tübingen, QUENSTEDT, 1867, Hdb. II-III, Oerlingen bei Ulm, Germany, Jurassic; 2, *L. paradoxa*, original specimen of MOERICKE, BSP AS III 316, Štramberg Limestone, Czech Republic, Tithonian (Upper Jurassic); 3, *L. paradoxa*, NHMW 1990/0041/4579, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 4, *L. paradoxa*, NHMW 1990/0041/3983, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 5, *L. paradoxa*, Jagiellonian University 127P 13, Woźniki, near Krakow, Tithonian (Upper Jurassic); 6, *Lecythocaris obesa* new species, holotype, NHMW 1990/0041/4126, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 7, *L. obesa*, paratype, NHMW 1990/0041/1330, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 8, *L. obesa*, paratype, NHMW 2007/0149/0002, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic). Scale bars = 1 mm.



three protuberances set in a triangle. The cardiac region extends to the furrow of the posterior margin and separates in half the branchial regions to their complete width. These obliquely directed mounds toward the cardiac region are formed less due to size than to the noticeable bounding margins. The as mentioned strongly inflated branchial region attains scarcely half the length of the cephalothorax and is set with strong pustules, among which the one on the outside especially identifies itself. Otherwise one sees small pustules, especially on the anterior part of the cephalothorax, that are especially distinctive. The posterior part of the cephalothorax is incised more in the center, and with a broad, smooth, marginal furrow.

From the white Jurassic chalk of the Oerlinger Thals; in WETZLER's Collection.

The tongue-shaped anterior prolongation [rostrum] is observed, only somewhat less well-developed, even in other perceived prosopids, particularly in *Prosopon heydeni*, *P. aequum*, *P. lingulatum*, *P. torosum*. The strong warting of the branchial region as found in *Prosopon torosum*, by which also in the incision in the outer margin, where the tongue-shaped prolongation begins, found in a similar way. In other species this incision is so flat, one could hardly call it an incision. However, under all united in the *Prosopon* form it exhibits its own characteristics permitting the hypothesis that it could be a particular genus, thus becoming for this case the name *Lecythocaris*, cylindrical crabs, not unsuitable to publish, and the species could be presented as *L. paradoxa*."

**Emended description:** Carapace small, slightly longer than wide or equidimensional; triangular with greatest width in posterior one-third; regions well defined as swollen elevations separated by deep, distinct grooves.

Rostrum broad, 43% maximum width measured at level of prominent protuberance at anterior corner of metabranchial region; spatulate, tapering slightly anteriorly, terminating in blunt anterior margin with shallow axial re-entrant; broadly sulcate axially and strongly downturned. Orbit circular and forward-directed; defined by deep, open notch at base of rostrum and distinct forward-directed rim at outer edge of orbit; fronto-orbital margin 70% maximum width. Anterolateral margin short, sinuous, narrowing from orbital margin to margin of hepatic region and convex around hepatic region. Posterolateral margin complexly convex; small protuberance on epibranchial margin lies just posterior to cervical groove; metabranchial region with prominent node marking level of maximum carapace width posterior to which the margin is convex. Posterior margin 46% maximum width, broadly concave.

Mesogastric region narrow; anterior process lanceolate, widest at midlength and bearing distinct axial crest; posterior part of mesogastric region an equilateral triangle. Protogastric region long, oval, with large nodose swelling at level at which mesogastric region broadens to triangular shape; not clearly separated from epigastric region. Hepatic regions prominent, globose swellings posterior to orbital rim and separated from gastric regions by deep groove. Cervical groove crosses midline in straight line and turns anterolaterally in straight line. Mesogastric region as broad as base of metagastric, swollen, with two subtle swellings laterally. Urogastric region with concave lateral margins, surface depressed. Cardiac region more or less triangular with apex at posterior margin; swollen anteriorly and somewhat depressed posteriorly; bearing three spines arrayed in a triangle; bounded laterally and posteriorly by distinct bran-

chiocardiac groove that nearly intersects posterior rim and that terminates before reaching lateral flanks. Epibranchial region a strong swelling just posterior to cervical groove. Mesobranchial region a larger, circular swelling posterior to hepatic region. An elongate branchial swelling lies posterior to mesobranchial swelling and adjacent to metagastric region, separated from it by deep pit. Metabranchial region an obliquely elongated, large, swollen region bearing pronounced spine on anterolateral corner and several moderately large nodes across surface. Entire surface of mold of interior of carapace with very fine granules. Surface of cuticle not preserved. Entire outer surface may have been finely spinose.

**Material examined:** Five specimens from the Ernstbrunn quarry localities, referred to *Lecythocaris paradoxa*, including NHMW 1990/0041/134, NHMW 1990/0041/1955, NHMW 1990/0041/3983, NHMW 1990/0041/4579, and NHMW 1990/0041/4824. In addition to the Ernstbrunn material, casts of specimens from three museums were also examined. They include the neotype, Museum Tübingen, QUENSTEDT 1867, Hdb. II-III, designated by WEHNER (1988); BSP AS III 316, illustrated by MOERICKE, 1897, pl. 6, fig. 12; and specimen 127P 13, identified as *Lecythocaris paradoxa strambergensis* by PATRULIUS (1959) and deposited in the Jagellonian University, Kraków, Poland.

**Measurements:** Measurements (in mm) are given in Table 6.

Table 6. Measurements (in mm) taken on the dorsal carapace of *Lecythocaris* spp. L1 = maximum carapace length; W1 = maximum carapace width; W2 = rostral width; W3 = fronto-orbital width; W4 = posterior width.

Specimen number	L1	W1	W2	W3	W4
<i>Lecythocaris paradoxa</i>					
Quenstedt Hdb II-II	2.9	2.4	1.1	1.7	1.4
BSP AS III 316	--	3.1	--	--	1.4
NHMW 1990/0041/134	--	4.0	1.7	2.5	--
NHMW 1990/0041/3983	5.2	6.1	2.0	3.3	~2.7
NHMW 1990/0041/4579	3.7	3.7	1.6	2.6	1.7
NHMW 1990/0041/4824	~3.2	4.2	--	--	--
<i>Lecythocaris obesa</i> new species					
NHMW 2007/0149/0002	6.6	6.6	2.3	3.2	2.5

**Discussion:** The emendation to the original description was based upon examination of several specimens from Ernstbrunn which seem to conform closely to the description of VON MEYER (1860). PATRULIUS (1959) compared the specimen from Munich, AS III 316, which was illustrated by MOERICKE (1897) with that from Kraków, 127P 13, and concluded that both differed perceptibly from the type species, as illustrated by VON MEYER (1860: pl. 23, fig. 31), in development of the protogastric tubercles. In recognition of the difference, he proposed a new subspecies, *Lecythocaris paradoxa strambergensis*. The type specimen illustrated by VON MEYER is apparently lost and a neotype has been designated by WEHNER (1988). Examination of these three specimens indicates that the differences between them are so subtle that they can be considered

within the limits of intraspecific variation. Without a larger sample to document that they represent different populations, it seems prudent to avoid use of the subspecies name proposed by PATRULIUS. Comparison of all the material confirms that all can be confidently referred to *L. paradoxa*.

The type species differs from the new species *Lecythocaris obesa* in having somewhat subdued development of the hepatic, epibranchial, and metabranchial swellings and development of a keel on the anterior projection of the metabranchial region in the type species.

***Lecythocaris obesa* nov. spec.**

Figs. 1.7, 6.6-6.8

**Diagnosis:** Carapace small, margin a series of globose swellings; with greatest width just posterior to midlength. Anterior process of metagastric region without keel. Protogastric and cardiac regions with small pustules. Hepatic, epibranchial, and metabranchial regions with extremely large, globose swellings.

**Description:** Carapace small, length and width about equal; margin a series of swellings with maximum width just posterior to midlength; regions well defined as swollen elevations separated by deep, distinct grooves.

Rostrum broad, 35% maximum carapace width measured at level of very large swelling at anterior corner of metabranchial region; spatulate, with convex lateral margins, terminating in broadly concave front; broadly sulcate axially and strongly downturned. Orbit circular and forward-directed, defined by deep, open notch at base of rostrum and distinct forward-directed rim at outer edge of orbit; lower orbital rim prominent with deep, open notch mesially; fronto-orbital width 48% maximum width. Anterolateral margin short, strongly convex around hepatic region. Posterolateral margin complex, with small epibranchial swelling, extremely large swelling at anterolateral corner of metabranchial region, and smoothly convex metabranchial margin posterior to it. Posterior margin 38% maximum width.

Mesogastric region very narrow; anterior process tapers anteriorly; axis smoothly rounded; posterior part of mesogastric region an equilateral triangle set with two lateral spines; protogastric region long, oval, depressed anteriorly and strongly swollen posteriorly; surface with fine nodes. Hepatic region a large, globose, pustulose swelling separated from orbital and gastric regions by prominent grooves. Cervical groove smoothly concave forward, well defined. Mesogastric region transversely oval, somewhat swollen laterally. Urogastric region extremely short, depressed. Cardiac region a large, circular, pustulose swelling; bounded laterally and posteriorly by distinct branchiocardiac groove which nearly intersects posterior rim and which terminates before reaching lateral flanks. Epibranchial region a strong, pointed swelling directed upward and outward at level above metabranchial swelling. Mesobranchial region apparently depressed. Elongate, slightly elevated branchial ridge lies between mesogastric and metabranchial regions, bounded by deep grooves. Metabranchial region with extremely large, globose swelling on anterolateral corner and finely nodose, uniformly swollen region posterior to it.

Entire surface of mold of interior of carapace with moderately large granules. Outer surface of cuticle with similar granules interspersed with very fine pustules. Entire surface may have been finely spinose.

**Measurements:** Measurements (in mm) are given in Table 6.

**Etymology:** The trivial name reflects the hypertrophied swellings that distinguish this species from the type species.

**Types:** The holotype, NHMW 1990/0041/4126, and five paratypes, NHMW 1990/0041/1330, NHMW 1990/0041/1846, NHMW 1990/0041/3104, NHMW 1990/0041/4077, and NHMW 2007/0149/0002.

**Occurrence:** The material was collected from the Ernstbrunn quarry localities.

**Discussion:** The extreme development of the hepatic, epibranchial, and metabranchial swellings and lack of development of a keel on the anterior projection of the metabranchial region serve to clearly distinguish *Lecythocaris obesa* from the type species.

#### Family Longodromitidae nov. fam.

**Included genera:** *Longodromites* PATRULIUS, 1959; *Abyssophthalmus* nov. gen.; *Planoprosopon* SCHWEITZER et al., 2007.

**Diagnosis:** Carapace longer than wide, widest at position of epibranchial or anterior-most branchial region, dorso-ventrally compressed; rostrum projected well beyond orbits, axially sulcate, markedly downturned distally; orbits shallow or deep, forward-directed, with intra- and outer-orbital spines as well as suborbital spines; protogastric and hepatic regions poorly differentiated; cervical groove deep, originating well posterior to outer-orbital spine; area between cervical and branchiocardiac grooves narrow; postcervical groove present, discontinuous and extending laterally about half the distance to the lateral margins or composed of two discrete segments that meet axially and extend laterally; cardiac region rounded triangular; epibranchial region with rounded or finger-like projection directed toward cardiac region; subhepatic swelling positioned below orbit, bounded by ventral extension of cervical groove and antennar groove; ventral extensions of cervical and branchiocardiac grooves meeting to form triangular subdorsal extension of epibranchial region; lateral sides short posteriorly as if they may have been poorly calcified.

**Discussion:** The combination of characters above cannot be accommodated by any other family within the Brachyura. The forward-directed orbits bounded by intra-, outer-, and suborbital spines are unique, as is the arrangement of carapace regions. In particular, the well-developed cervical and branchiocardiac grooves which bound a short length of the dorsal carapace is unique. The genera that are here referred to the family are quite similar to one another in many regards but are easily differentiated by details of ornamentation and carapace shape. Particularly notable is the shortening of the lateral sides that is similar to some species of *Pithonoton* and modern homolodromiids, which have poorly calcified areas in the lateral branchial regions of the carapace.

**Key to genera of the Longodromitidae nov. fam.:**

- 1a. Orbits shallow, orbital ornamentation reduced, carapace extremely dorso-ventrally compressed ..... *Planoprosopon*  
 1b. Orbits deep, orbital ornamentation strong, carapace moderately dorso-ventrally compressed. .... 2  
 2a. Carapace ovate or rectangular, regions flattened and moderately defined by shallow to medium grooves; rostrum axially sulcate appearing markedly bilobate ..... *Longodromites*  
 2b. Carapace rectangular, regions inflated and well defined by deep grooves; rostrum well defined but not markedly bilobate ..... *Abyssophthalmus* nov. gen.

**Genus *Longodromites* PATRULIUS, 1959**

**Type species:** *Prosopon angustum* REUSS, 1858, by original designation.

**Included species:** *Longodromites angustus*; *L. bicornutus* MUȚIU & BĂDĂLUȚĂ, 1971; *L. excisus* (VON MEYER, 1857), as *Prosopon*; *L. ovalis* (MOERICKE, 1897), as *Prosopon*.

**Diagnosis:** Carapace with parallel or convex lateral margins, longer than wide, widest at position of epibranchial or anterior-most branchial region; regions not well-differentiated; ornamentation granular if present; orbits large, deep, forward directed, with intra-, outer-, and suborbital spines; rostrum projected well beyond orbits, axially sulcate, tip markedly downturned; cervical groove deep; branchiocardiac groove shallow; area between cervical and branchiocardiac grooves narrow; postcervical groove present, variable in development; distinct subhepatic swelling bounded by cervical and antennar grooves.

**Discussion:** *Longodromites* is well known from Jurassic rocks of central and eastern Europe and is represented by four described species. Most diagnostic and distinctive are the large, forward-directed orbits that typify all of the species as well as the relatively unornamented carapace and narrow area between the cervical and branchiocardiac grooves. Presence of three distinct species from the Ernstbrunn localities suggests that niche partitioning may have occurred within the genus as has been reported for *Goniodromites* (SCHWEITZER & FELDMANN, 2008 [imprint 2007]).

***Longodromites angustus* (REUSS, 1858)**

Figs. 1.6, 7.4-7.7

- 1858 *Pithonoton angustum* REUSS, 1858, p. 11.  
 1858 *Prosopon angustum* – VON MEYER, p. 208.  
 1859 *Pithonoton angustum* – REUSS, p. 72, pl. 24, fig. 3.  
 1895 *P. [Prosopon] angustum* REUSS – REMEŠ, p. 203, pl. 2, fig. 10.  
 1897 *Prosopon anjustum* REUSS – Moericke, p. 61.  
 1929 *P. [Pithonoton] angustum* V. MEYER – GLAESSNER, p. 319.  
 1933 *P. [Pithonoton] ? angustum* V. MEY. – GLAESSNER, p. 181.  
 1959 *Longodromites angustus* (REUSS, 1858) – PATRULIUS, p. 254, fig. 1a.  
 1966 *Longodromites angustus* (REUSS, 1858) – PATRULIUS, 1966, p. 514, pl. 31, figs. 25, 26.



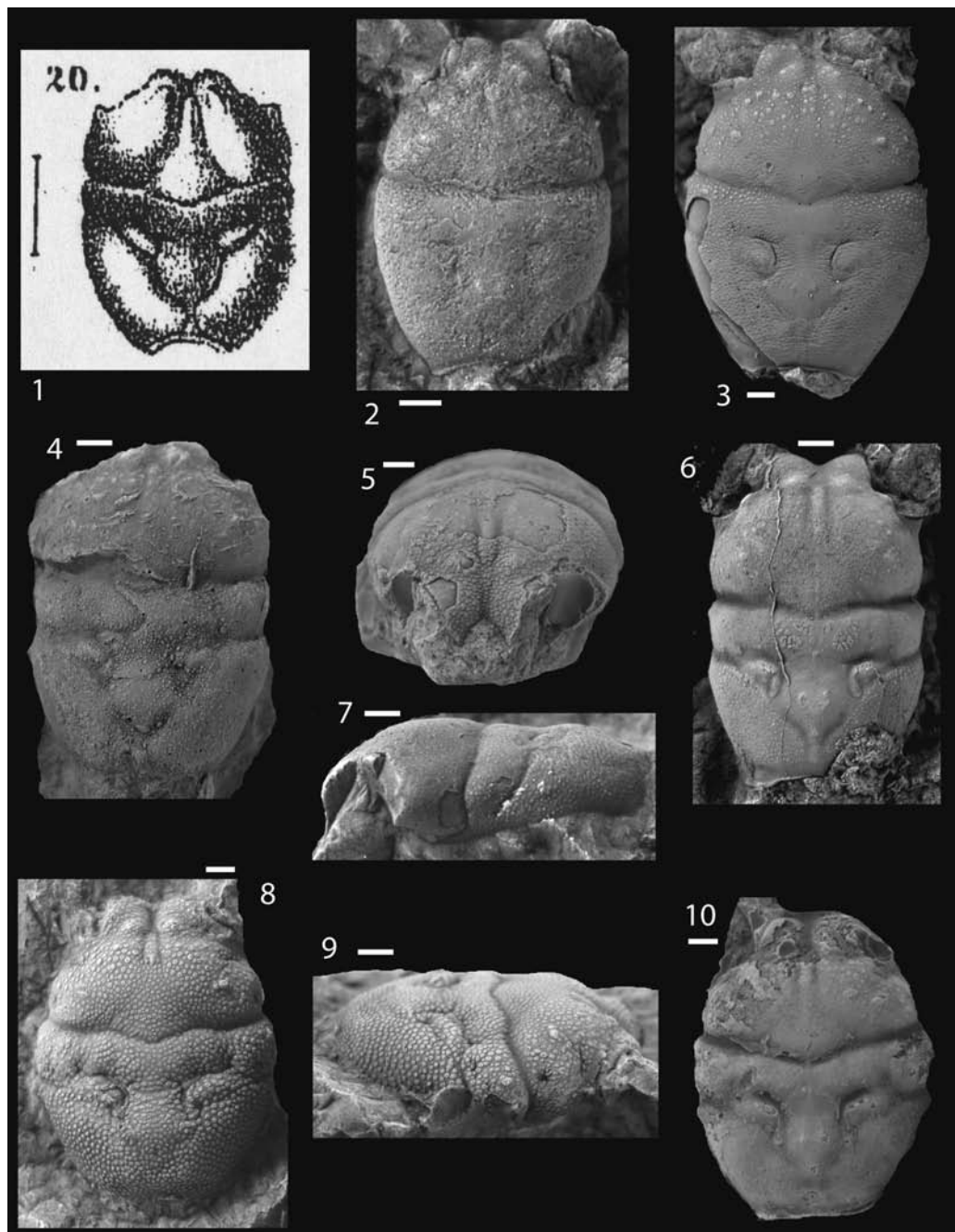


Fig. 7. *Longodromites* spp. 1, *Longodromites excisus*, digital image from VON MEYER (1860: pl. 23, fig. 20); 2, *L. excisus*, NMHW 1990/0041/4327, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *L. excisus*, NMHW 1990/0041/5060, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 4, *Longodromites angustus*, cast of holotype, GSA 2357, Štramperk Limestone, Czech Republic, Tithonian (Upper Jurassic); 5, *L. angustus*, ►

**Original description** (translated from REUSS 1859: 72): “This species is indeed very similar to *P. rostratum* v. Meyer, however, it distinguishes itself indeed at first sight by means of its much smaller width. The cephalothorax is 0.47” long, however only 0.3” wide. Length and width, in this case, is therefore 1.56:1. The outline is almost elongated-foursided, in which the lateral margins proceed almost parallel. Therefore, the carapace is for the most part of its length almost equally wide, narrowing first in the hind one-third somewhat. The posterior margin is only 0.18” wide. The rostrum forms, it appears, as a triangle, with acuminate longitudinally furrowed flaps; however, the spine on the example under consideration is broken off. The lateral parts of the anterior margins are incised by means of the orbits, which are separated by 0.16”.

Likewise here the surface of the carapace is divided into three parts by means of two transverse grooves, which proceed entirely straight and transversely. The front is almost symmetrically vaulted; only along the axis a very sharp and narrow triangular field comes forward and is very weakly raised. Upon this anterior, narrow, beak-shaped prolongation are perceptible two small round swellings behind one another. In front of the strongly lengthened but not reaching the rostrum prolongation [mesogastric region] stands on each side likewise a small swelling [epigastric regions].

The middle part is laterally very short, in the middle it is lengthened to an almost triangular, backward-directed flap, which intervenes deep into the posterior region of the carapace [cardiac region]. It is separated from the region lying in front of it by means of a distinct transverse furrow [postcervical groove] and is rather vaulted and defined laterally by means of deep grooves. The remaining part of the middle region of the carapace is almost level, only the middle is barely perceptibly raised.

The hind part of the cephalothorax is divided in half by means of the before-mentioned triangular prolongation of the middle field and a median furrow proceeding from it; the two halves themselves have no further organization noticeable.

Of the shell no trace is preserved, however the steinkern indicates that its upper surface had been ornamented with dense, very small tubercles. Most apparently they are distinct in the front section of the cephalothorax.”

**Emended description:** Carapace longer than wide, width about two-thirds maximum length, widest at epibranchial region just posterior to intersection of cervical groove with margin, about 70 percent the distance posteriorly on carapace; carapace flattened longitudinally and moderately vaulted transversely; carapace regions defined as broad swellings separated by moderately deep grooves.

Rostrum extending well beyond orbits, strongly downturned so that distal half is perpendicular to proximal half, tip concave; surface axially sulcate; width about 45 percent

- NMHW 2007z0162/001; 6, *L. angustus*, NHMW 1990/0041/3190, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 7, *L. angustus*, NHMW 1990/0041/2691, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 8, *Longodromites ovalis* NHMW 1990/0041/230; 9, *L. ovalis*, NHMW 1990/0041/230, lateral view, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 10, *L. ovalis*, cast of holotype, original specimen of MOERICKE (1897), BSP AS III 311, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic). Scale bars = 1 mm. Scale bar in VON MEYER illustration is of unknown length, but possibly indicates original size of fossil.

maximum carapace width. Orbits deep, forward directed, bounded on inner orbital angle by rostrum; with blunt intra-orbital spine; outer-orbital spine short, triangular, directed anterolaterally; sub-intraorbital spine separated from outer-orbital spine by fissure, broad; sub-innerorbital spine short, triangular.

Lateral margins overall parallel, maintaining approximately same width throughout length, constricted at intersection of cervical and branchiocardiac groove with margin, narrowing posteriorly. Posterior margin concave.

Epigastric regions small, equant. Protogastric and hepatic regions not well differentiated from one another, protogastric somewhat more inflated. Mesogastric region with long anterior process, process terminating between epigastric regions, widening distally, without obvious ornament. Metagastric region very long, not well differentiated from epibranchial regions lateral to it. Urogastric region narrow, short, depressed below level of metagastric and cardiac regions. Cardiac region rounded triangular, apex directed posteriorly. Intestinal region not well differentiated.

Cervical groove overall relatively straight, with weak inflection around posterior margin of mesogastric region, deepest laterally. Branchiocardiac groove extending weakly obliquely posteriorly, deepest laterally, weakening axially. Postcervical groove deep, parallel to branchiocardiac groove.

Epibranchial region most strongly inflated laterally, with inflated, finger-like projection axially, projection bounded anteriorly by postcervical groove and posteriorly by branchiocardiac groove. Remainder of branchial regions undifferentiated. Regions appearing to have been uniformly finely granular.

Subhepatic region weakly inflated, situated beneath orbit, bounded by ventral extension of cervical groove on posterior margin and antennar groove on ventral margin. Ventral extension of epibranchial region with a marked swelling, bounded by ventral extensions of cervical and branchiocardiac grooves. Remainder of lateral sides short; may have been weakly calcified.

**Measurements:** Measurements (in mm) taken on specimens of *Longodromites angustus* are given in Table 7.

Table 7. Measurements (in mm) taken on the dorsal carapace of *Longodromites* spp. L1 = maximum carapace length; W1 = maximum carapace width; L2 = length to position of maximum width; W2 = rostral width; W3 = fronto-orbital width.

Specimen number	L1	W1	W2	W3	L2
<i>Longodromites angustus</i>					
NHMW 2007/0149/0009	14.9	9.5	4.8	9.4	9.8
NHMW 1990/0041/2691	9.4	6.3	2.2	6.0	6.0
NHMW 1990/0041/1903	6.0	-	-	-	-
NHMW 1990/0041/3126	7.4	5.3	-	4.8	5.3
NHMW 2007z0162/0001	12.7	8.4	3.4	8.4	9.2
NHMW 1990/0041/3190	9.0	5.9	3.0	5.8	6.6

Specimen number	L1	W1	W2	W3	L2
<i>Longodromites ovalis</i>					
NHMW 1990/0041/230	13.0	10.	3.9	7.6	7.8
NHMW 1990/0041/236	10.5	8.0	3.2	5.4	6.9
NHMW 1990/0041/3042a	12.6	10.9	-	-	7.9
NHMW 1990/0041/231	13.8	12.6	4.7	8.4	8.8
BSP AS III 311 holotype (cast)	10.9	8.6	4.0	5.6	6.7
<i>Longodromites excisus</i>					
NHMW 1990/0041/4327	7.0	4.9	2.3	4.3	3.8
NHMW 1990/0041/5063	13.6	10.5	4.2	7.4	8.3
NHMW 1990/0041/5060	13.5	9.6	3.6	8.0	8.0

Type: GSA 2357, holotype.

Material examined: NHMW 1990/0041/1903, NHMW 1990/0041/2691, NHMW 1990/0041/3126, NHMW 1990/0041/3190, NHMW 2007/0149/0008, NHMW 2007/0149/0009, NHMW 2007z0162/0001; BM In.28148, identified by M. F. GLAESSNER in 1930.

Occurrence: The holotype was collected from the Štramberg locality. The NHMW specimens were collected from the Ernstbrunn quarry localities.

Discussion: The referred specimens agree well with the holotype and original description. WEHNER (1988) and MÜLLER et al. (2000) considered that *Longodromites excisus* was the type species of *Longodromites*, apparently based upon WEHNER's synonymy of *Longodromites angustus*, *L. ovalis*, and *L. excisus*. PATRULIUS (1959) clearly designated what he called *Pithonoton angustum* (originally *Prosopon*) as the "genotype" for the new genus. We do not consider that the three species mentioned are synonymous; thus, *L. angustus* stands as the type species.

***Longodromites ovalis* (MOERICKE, 1897)**

Figs. 7.8-7.10

- 1897 *Prosopon ovale* MOERICKE, p. 65, pl. 6, fig. 16.
- 1895 *P. ovale* MÖRICKE – REMEŠ, p. 203, pl. 3, fig. 16.
- 1924 [imprint 1925] *Avihomeola ovalis* (MOERICKE, 1889 [error pro 1897]) – VAN STRAELEN, p. 346.
- 1929 *N. [Nodoprosopon] ovale* (MOERICKE), 1889 [error pro 1897] – GLAESSNER, p. 272.
- 1988 *Longodromites excisus* (VON MEYER, 1857). – WEHNER, p. 114, fig. 30c.

Diagnosis: Carapace ovate, width about 80 percent maximum width; fronto-orbital width about 70 percent maximum carapace width; postcervical groove segments long, beginning two-thirds the distance laterally, extending weakly obliquely toward axis in sinuous path; metagastric region long, much wider than mesogastric region, broadly V-shaped, well separated from epibranchial regions lateral to it.

**Description:** Carapace ovate, longer than wide, width about 80 percent maximum length, widest at position of branchial region just posterior to intersection of branchiocardiac groove with lateral margin about 60 percent the distance posteriorly on carapace. Carapace flattened transversely and longitudinally, densely ornamented with large granules.

Rostrum projected well beyond orbits, downturned distally, axially sulcate, about 40 percent maximum carapace width. Orbits deep, directed forward, bounded on inner orbital angle by rostrum; blunt intra-orbital projection; outer orbital spine very short, poorly developed, directed forward, wrapping around suborbital margin, separated from sub-intraorbital spine by closed fissure; sub-intraorbital spine broad; fronto-orbital width about 70 percent maximum carapace width.

Lateral margins convex, constricted at intersection of cervical and branchiocardiac grooves with margin, narrowing markedly anteriorly and posteriorly, posterior margin rimmed, straight to weakly concave.

Epigastric regions spherical, markedly inflated. Protogastric regions not well differentiated from hepatic regions, with a few scattered larger tubercles. Mesogastric region with long anterior process, widening distally, without notable ornamentation. Metagastric region long, much wider than mesogastric region, broadly V-shaped, well-separated from epibranchial regions lateral to it. Urogastric region narrow, short, depressed below level of metagastric and cardiac regions. Cardiac region rounded-triangular, moderately inflated.

Cervical groove sinuous, deepest laterally, concave forward along posterior margin of hepatic and protogastric regions, then arcing forward and then concave forward around posterior margin of mesogastric region. Postcervical groove segments long, beginning two-thirds the distance laterally, extending weakly obliquely toward axis in sinuous path. Branchiocardiac groove weak, deepest laterally, extending obliquely posteriorly toward cardiac region.

Epibranchial region inflated laterally and extending in fingerlike projection axially. Remainder of branchial regions not differentiated, not strongly inflated. Subhepatic region moderately inflated, bounded posteriorly by deep ventral extension of cervical groove and ventrally by antennar groove.

**Measurements:** Measurements (in mm) taken on specimens of *Longodromites ovalis* are presented in Table 7.

**Type:** BSP AS III 311, original specimen of MOERICKE (1897), interpreted to be the holotype.

**Material examined:** NHMW 1990/0041/230, NHMW 1990/0041/231, NHMW 1990/0041/236, NHMW 1990/0041/3042a.

**Occurrence:** The additional referred material was collected from the Ernstbrunn quarry localities.

**Discussion:** WEHNER (1988) considered this species to be a subspecies of *Longodromites excisus*. It is clearly a unique form and stands as a separate species based upon its markedly ovate carapace shape; broadly V-shaped metagastric region; granular dorsal carapace ornamentation; and relatively narrow fronto-orbital width compared to other species.



***Longodromites excisus* (VON MEYER, 1857)**

Figs. 7.1-7.3

- 1857 *Prosopon excisum* VON MEYER, p. 556.  
 1860 *Prosopon excisum* – VON MEYER, p. 207, pl. 23, fig. 20.  
 1966 *Longodromites excisus* (MEYER, 1857) – PATRULIUS, p. 515.  
 2000 *Longodromites excisus* (VON MEYER, 1857) – MÜLLER et al., fig. 18G.

**Diagnosis:** Carapace wider than long, width about 75 percent maximum carapace length; regions in general flattened and poorly differentiated, especially epigastric, protogastric, hepatic region not differentiated, ornamented anteriorly with scattered granules of varying sizes; mesogastric region weakly defined, with long anterior process, widening distally; cardiac region rounded-triangular, flattened.

**Description:** Carapace longer than wide, width about 75 percent maximum carapace width, widest at position of branchial region just posterior to intersection of branchiocardiac groove with lateral margin; carapace flattened longitudinally and moderately vaulted transversely.

Rostrum projected well beyond orbits, steeply downturned distally so as to be perpendicular to proximal part, tip blunt triangular, surface axially sulcate, maximum width about 40 percent maximum carapace width. Orbits directed forward, bounded on inner angle by rostrum, with blunt intraorbital projection, outer-orbital spine short, directed anterolaterally, wrapping around under suborbital surface, separated from sub-intraorbital spine by fissure, fronto-orbital width about 85 percent maximum carapace width.

Lateral margins convex, constricted where intersected by cervical and branchiocardiac grooves, narrowing anteriorly and posteriorly. Posterior margin narrowly rimmed, concave.

Epigastric regions equant, weakly inflated. Protogastric and hepatic region not differentiated, ornamented anteriorly with scattered granules of varying sizes. Mesogastric region weakly defined, with long anterior process, widening distally. Metagastric region wider than mesogastric region, long, flattened. Urogastric region long, narrow, with concave lateral margins. Cardiac region rounded-triangular, flattened. Intestinal region very weakly depressed below level of cardiac region.

Cervical groove sinuous, deepest laterally, concave forward initially, then curving concavely to terminate in pores axially. Postcervical groove segments short, deep, bounding posterolateral margins of metagastric region. Branchiocardiac groove very poorly developed, deepest laterally, extending toward cardiac region and becoming very weak.

Epibranchial regions inflated laterally, with rounded projection axially bounded by branchiocardiac and postcervical grooves. Branchial region not inflated, with weak, scabrous ornament.

Subhepatic region moderately inflated, bounded posteriorly by deep ventral extension of cervical groove and ventrally by antennar groove. Remainder of lateral side short as if it may have been weakly calcified.

**Measurements:** Measurements (in mm) taken on the dorsal carapace of *Longodromites excisus* are given in Table 7.

**Type:** Neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 38.

**Material examined:** NHMW 1990/0041/2818, NHMW 1990/0041/4327, NHMW 1990/0041/5060, NHMW 1990/0041/5063.

**Occurrence:** The additional referred material was collected from the Ernstbrunn quarry localities.

**Discussion:** *Longodromites excisus* is differentiated from other species in the genus by its circular epibranchial extensions; moderately broad fronto-orbital width; and weakly convex lateral margins of the carapace. In addition, the regions of the carapace are flattened in this species rather than being inflated as seen in *L. ovalis* and *L. angustus*.

### Genus *Abyssophthalmus* nov. gen.

**Type species:** *Prosopon spinosum* VON MEYER, 1842.

**Included species:** *Abyssophthalmus mirus* (MOERICKE, 1897), as *Prosopon*; *A. spinosus*; *Abyssophthalmus stotzingensis* (VON MEYER, 1856), as *Prosopon*.

**Diagnosis:** Rostrum long, straight sided, extending well beyond orbits; orbits deep, directed forward, bounded by intra-orbital, outer-orbital, and suborbital spines; outer-orbital spine long, prominent, directed forward; cervical and branchiocardiac grooves well developed; postcervical groove composed of two discrete segments, nearly continuous, extending laterally and crossing axis to bound anterior margin of cardiac region; lateral margins parallel sided, maximum width at mid-length; subhepatic region well developed, situated below orbit.

**Etymology:** The genus name is derived from the Greek word *abyssos* meaning “a deep pit”, and the Greek word *ophthalmos* meaning eye, in reference to the deep, well-developed orbits in the taxon, unusual in Jurassic brachyurans. The gender is masculine.

**Discussion:** The type species of the new genus was originally referred to *Prosopon* and then later referred to *Nodoprosopon*. Neither genus can accommodate the large, forward-directed, deep orbits present in the species nor can they accommodate the parallel-sided, elongate shape of the carapace seen in the type species. Thus, the new genus is warranted. Such well-defined, deep orbits have not been described before for a Jurassic brachyuran.

### *Abyssophthalmus spinosus* (VON MEYER, 1842) nov. comb.

Figs. 8.1, 8.5-8.7

- 1842 *Prosopon spinosum* VON MEYER, p. 71, fig. 1, 2.
- 1860 *Prosopon spinosum* – VON MEYER, p. 196, pl. 23, figs. 6, 7.
- 1925 *Prosopon spinosum* H. v. MEYER – BEURLIN, p. 487.
- 1929 *N. [Nodoprosopon] spinosum* (VON MEYER, 1842) – GLAESSNER, p. 273.
- 1933 *N. [Nodoprosopon] spinosum* (V. MEY.) – GLAESSNER, p. 180.
- 1936 *Prosopon* (*Avihomola* bzw. *Nodoprosopon*) *spinosum* H. v. MEYER – KUHN, p. 122, fig. 2.
- 1969 *Nodoprosopon spinosum* (V. MEYER) – FÖRSTER, p. 53, pl. 2, fig. 2.
- 1988 *Nodoprosopon spinosum* (VON MEYER, 1842) – WEHNER, p. 44, pl. 2, figs 9, pl. 3, figs. 1, 2.
- 2000 *Nodoprosopon spinosum* (VON MEYER) – MÜLLER et al., fig. 17f.
- 2007 *Prosoopon spinosum* V. MEYER – SCHWEITZER et al., p. 110.

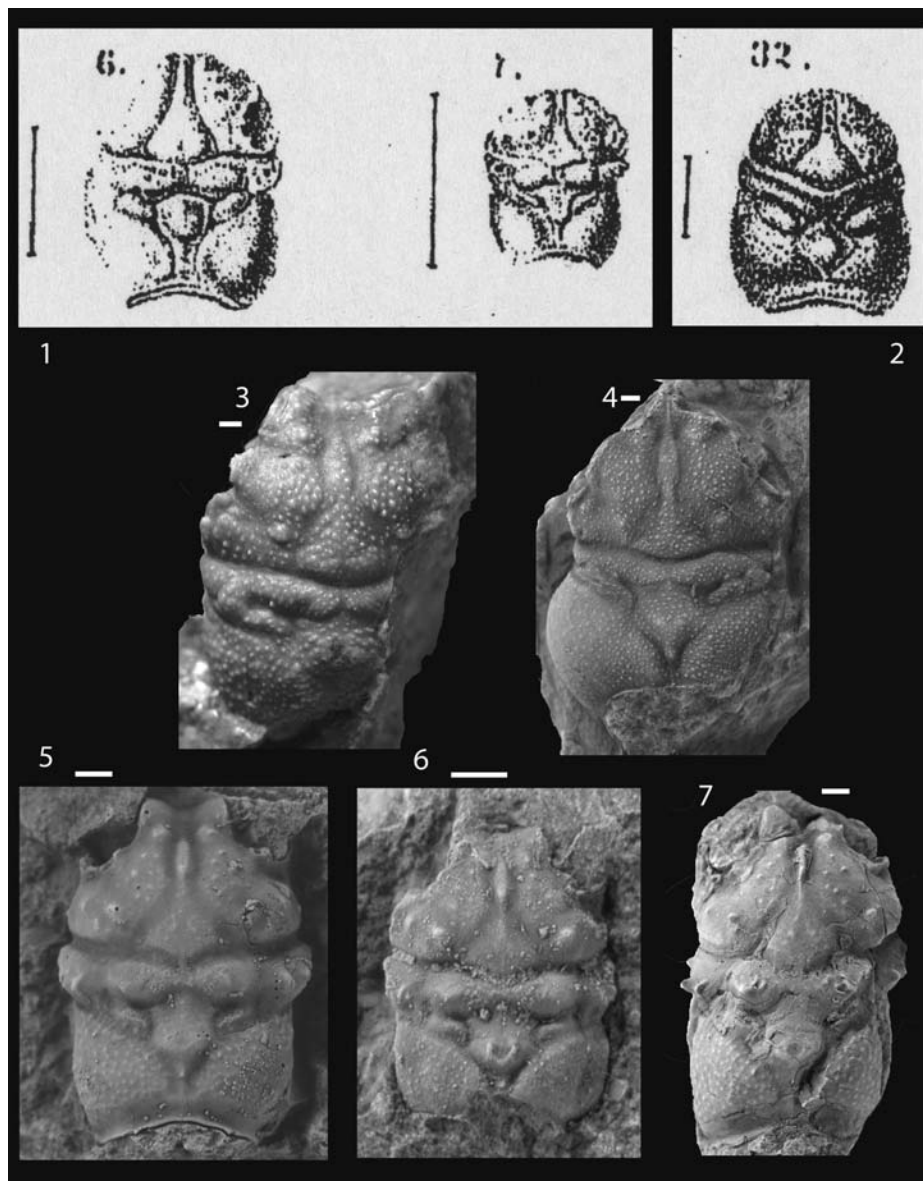


Fig. 8. *Abyssophthalmus* spp. 1, *Abyssophthalmus spinosus*, digital image from VON MEYER (1860: pl. 23, figs. 6, 7); 2, *A. stotzingensis*, digital image from VON MEYER (1860: pl. 23, fig. 32); 3, *A. mirus*, holotype, original specimen of Moericke (1897), BSP AS III 315, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic); 4, *A. mirus*, SMNS 61671, note large bopyrid swelling in left branchial chamber, Jurassic; 5, *A. spinosus*, neotype, BSP 1980 XXX 528, Biburg, Germany, Oxfordian (Upper Jurassic); 6, *A. spinosus*, BSP 1980 XXX 726, Biburg, Germany, Oxfordian (Upper Jurassic); 7, *A. spinosus*, BSP 1980 XXX 687, Biburg, Germany, Oxfordian (Upper Jurassic). Scale bars = 1 mm. Scale bars in VON MEYER illustrations are of unknown length, but possibly indicates original size of fossil.

**Original description** (translated from VON MEYER 1860: 196): "Of two examples one cephalothorax measures 0.009 long and 0.0075 (units for these measurements unknown) wide, for which in the other obtains 0.0125 and 0.01. The maximum width falls in the middle region. The half circular front region is shorter than the half length of the cephalothorax. The not remarkably strong, but sharply defined gastric region leads to the weakly incised front end, behind it is not crenated, yet it is supplied with hints of a pair of swellings. The hepatic region is within and behind inflated and decorated with a row of strong warts, of which the latter are somewhat larger and tend to be spiny. In the transverse furrow lies a pair of pores. Of the genital region the outward swelling is decorated with three sharp warts; the middle region consists of a pair of transversely oval, not sharply separated swellings with weak tubercles. The swelling which is obliquely directed toward the cardiac region is, like the cardiac region which is more triangular formed and proceeding hindwards in a thin process, strongly delimited and pushes not as in other *Prosoponids* forward but on the contrary posteriorly on the outer corners of the cardiac region. The posterior part is itself outwardly short and in back broadly separated. The incision for the reception of the abdomen is clear, extending along the entire posterior margin, and is bounded with a groove. Under the hand lens one detects that the shell of the front and middle regions is ornamented with shallow rounded impressions, which in the posterior region usually have an inflated edge, and give the presentation of small, centrally impressed, warts.

From the upper white Jurakalk of Aalen in Württemberg; in the Münster collection."

**Emended description:** Carapace longer than wide, width about 66 to 80 percent maximum length, width greater in smaller specimens and narrower in larger specimens; widest at about half the distance posteriorly; carapace moderately vaulted transversely and flattened longitudinally; regions well marked by wide grooves.

Rostrum projected well beyond orbits; straight sided, rimmed; anterior margin concave; axially sulcate; eyestalk appearing to have arisen from below rostrum; rostral width about one-third to 40 percent maximum carapace width. Orbits deep, directed forward, rimmed; bounded on upper inner angle by rostrum; intra-orbital spine short, broadly triangular; outer-orbital spine long, triangular, directed forward; inner suborbital spine blunt, separated from outer-suborbital spine by broad notch; outer-suborbital spine triangular; fronto-orbital width about 85 percent maximum carapace width.

Lateral margins overall parallel; segment anterior to intersection of cervical groove convex; segment between cervical and branchiocardiac grooves strongly convex, with tubercles; segment posterior to branchiocardiac groove weakly convex. Posterior margin of carapace concave, broadly rimmed.

Epigastric regions small, equant. Protogastric regions elongate, ornamented with tubercles. Mesogastric region with long anterior process, oblong swelling or keel on anterior process, process terminating between epigastric regions; broadening posteriorly into small triangular area. Metagastric region bilobed, axially constricted, may be keeled transversely in smaller specimens. Urogastric region deeply depressed, with convex anterior and posterior margins. Cardiac region inflated, rounded-triangular with apex directed posteriorly. Intestinal region poorly defined. Hepatic region ovate, ornamented with large tubercles.

Cervical groove overall relatively straight, deepest laterally. Branchiocardiac groove directed very weakly obliquely posteriorly, deepest laterally, weakening along margins of cardiac region.

Epibranchial region strongly inflated laterally; with large tubercles, with much more weakly inflated, finger-like projection directed at cardiac region. Remainder of branchial region broadly inflated, densely ornamented with medium-sized tubercles.

Subhepatic region inflated, positioned beneath orbit, bounded by cervical groove posteriorly and ventrally by antennar groove. Epibranchial region extending onto lateral side, bounded by cervical and branchiocardiac grooves. Remainder of lateral side short, possibly as if uncalcified posteriorly as in extant Homolodromiidae.

**Neotype:** BSP 1980 XXX 528, designated by WEHNER (1988). The holotype is apparently lost. We were unable to locate it in an exhaustive search. VON MEYER's original specimens were collected from Aalen, not far from Stuttgart, from Upper Jurassic spongiolithic rocks of Oxfordian age (*planula* Zone) (G. SCHWEIGERT, personal communication, September, 2007). WEHNER's neotype was collected from Biburg, near Eichstätt, about 80 km from the type locality, from Oxfordian rocks, also of the *planula* Zone (G. SCHWEIGERT, personal communication, September, 2007). WEHNER's (1988) neotype agrees well with the illustration and rather short 1860 description of VON MEYER. Because the original type material for *Prosopon spinosum* is missing, we accept WEHNER's (1988) neotype, even though it is from a different locality. The rocks are of the same age. The brachyuran assemblage at the two localities is reportedly very similar as well, based on specimens in private collections (G. SCHWEIGERT, personal communication, September, 2007).

**Material examined:** BSP 1980 XXX 725-731, BSP 1980 XXX 687, BSP 1980 XXX 753-756; SMNS 67179.

**Measurements:** Measurements (in mm) taken on specimens of *Abyssophtalmus spinosus* are presented in Table 8.

Table 8. Measurements (in mm) taken on the carapace of *Abyssophtalmus spinosus*. L1 = maximum carapace length; W1 = maximum carapace width; L2 = length to position of maximum width; W2 = rostral width; W3 = fronto-orbital width.

Specimen number	L1	W1	W3	W2	L2
BSP 1980 XXX 687	18.7	12.2	10.4	4.8	10.3
BSP 1980 XXX 726	5.6	4.4	3.8	1.6	3.0
BSP 1980 XXX 727	5.2	3.9	3.6	1.4	2.4
BSP 1980 XXX 755	12.0	8.6	7.4	2.9	6.0
BSP 1980 XXX 756	7.8	5.6	5.2	-	4.0
SMNS 67179	9.8	8.4	6.6	1.6	5.0
Cast of neotype, BSP 1980 XXX 528	11.8	7.5	6.4	2.6	5.4

**Discussion:** The carapace morphology among specimens of *Abyssophtalmus spinosus* is quite variable. At least some of this variability seems to be attributable to allometric growth (Table 8). Smaller specimens exhibit a width that is a greater percent-



age of the maximum length, giving them an overall more equant appearance. Larger specimens are more elongate in shape. In addition, smaller specimens seem to have more pronounced ornamentation, especially in the form of a keeled metagastric region, whereas larger specimens lack keels on this region. Because all of the measured and examined specimens were collected from the same locality and appear to be from the same lithology, it seems likely that they belong to the same species, especially given that the differences seem to track changes in size.

***Abyssophtalmus stotzingensis* (VON MEYER, 1856) nov. comb.**

Fig. 8.2

- 1856 *Prosopon stotzingense* VON MEYER, p. 51.
- 1860 *Prosopon Stotzingense* – VON MEYER, p. 197, pl. 23, fig. 32.
- 1924 [imprint 1925] *Avihomola stotzingensis* (VON MEYER, 1856) – VAN STRAELEN, p. 347.
- 1929 *N. [Nodoprosopon] ? stotzingense* (V. MEYER, 1856) – GLAESSNER, p. 273.
- 1933 *N. [Nodoprosopon] ? stotzingense* (V. MEY.) – GLAESSNER, p. 180.
- 1988 *Nodoprosopon ? stotzingense* (VON MEYER, 1860) – WEHNER, p.62.
- 2007 *Prosopon stotzingense* V. MEYER – SCHWEITZER et al., p. 110.

**Original description** (translated from VON MEYER 1860: 197): “The cephalothorax, which I know from this species, measures 0.0055 length and not over 0.004 (units for these measurements unknown) maximum width, which falls in the posterior half. The semicircular front part is shorter than half the length of the cephalothorax. The narrow continuation of the sharply defined gastric region is decorated with a distinct wart and appears to lead almost up to the front end of the cephalothorax, which will have been incised. The hepatic region possesses scarcely perceptible tubercle-formed inflations and is, as is the cephalothorax generally, with small warts, among which none are particularly noticeable. The genital region is narrow in shape, and in the posterior is scarcely separated from the transverse furrow. The somewhat inflated, rhomboid cardiac region is not stemmed and well developed which is also true of both the mounds directed toward it. The branchial region measures outside more than half the length of the cephalothorax; and in the posterior borders the two halves hardly touch. It is, like the front part, decorated with many small warts, which (the warts) in the genital and cardiac regions weakly occur. The posterior margin is less deeply than widely notched and rimmed with a weak furrow, in front of it lies a wide furrow which toward the lateral margins gradually disappears, which appears to be warted.

The species stands near *Prosopon spinosum*, from which it is however thus different, that of its largest width falls in the hind half, that in the front and middle part the spine-warts are absent, that the whole shell appears to be warted, and that the urogastric and the angle directed toward the anterior corner of the cardiac region are particularly developed which is defined by the cardiac region.”

**Material:** Unfortunately, there is no known material referable to this species. The type was not found in the collections in Munich. The type locality is Nieder-stotzingen, which is 24 km north-east of Ulm, Germany.

**Discussion:** WEHNER (1988) questionably referred the species to *Nodoprosopon*, in which it cannot be accommodated due to the elongate, triangular nature of species of *Nodoprosopon* (SCHWEITZER et al. 2007). VON MEYER (1860) noted that the species was quite similar to *Prosopon spinosum*, and details of the description and his illustration (VON MEYER 1860: pl. 23, fig. 32) confirm this. Both species exhibit a broadly concave, rimmed posterior margin and well developed metagastric, urogastric, and epibranchial regions. Thus, we refer *P. stotzingense* to *Abyssophthalmus*; recovery of the type specimens or referable material from the type locality could help confirm this placement.

***Abyssophthalmus mirus* (MOERICKE, 1897) nov. comb.**

Figs. 8.3, 8.4

- 1897 *Prosopon mirum* MOERICKE, p. 60, pl. 6, fig. 14.
- 1924 [imprint 1925] *Avihomeola mira* (MOERICKE, 1889 [error pro 1897]) – VAN STRAELEN, p. 347.
- 1929 *Nodoprosopon mirum* (MOERICKE, 1889 [error pro 1897]) – GLAESSNER, p. 272.
- 1988 *Nodoprosopon mirum* (MOERICKE, 1889 [error pro 1897]) – WEHNER, p. 57, pl. 4, figs. 3-5.
- 2000 *Nodoprosopon mirum* (MOERICKE) – MÜLLER et al., fig. 17I.

**Original description** (translated from MOERICKE 1897: 60-61): “The rather uniformly wide carapace extends in a very strongly curved rostrum. Of the triangular gastric region the posterior part is a little crenate; the anterior narrow end is very long. The hepatic region which lies next to the margin of the gastric consists of three tubercles decorated with different sized warts. The lateral margins of the upper part of the carapace are decorated with spine-shaped projections. The middle part of the cephalothorax situated between both transverse furrows is only a narrow band, of which a small swelling is drawn out toward the cardiac region. The cardiac region is shaped as a rather large pentagon, which is with an angle directed toward the posterior margin of the carapace. The steinkern leaves on its upper surface a quantity of small warts.”

**Type:** The original specimen of MOERICKE (1897), interpreted to be the holotype, is BSP AS III 315.

**Material examined:** SMNS 61671, a large specimen with bopyrid swelling in the left branchial region.

**Discussion:** The original specimen of MOERICKE (1897) maintained in the BSP is fragmentary; thus, MOERICKE’s illustration is apparently a reconstruction (MOERICKE 1897: pl. 6, fig. 14). The narrow area between the cervical and branchiocardiac grooves; confluent protogastric and hepatic regions; and forward-directed orbits with intra- and outer-orbital spines, all mentioned in MOERICKE’s original description, suggest that *Prosopon mirum* is a member of *Abyssophthalmus*.

Genus *Planoprosopon* SCHWEITZER, FELDMANN, & LAZÄR, 2007

Type species: *Prosopon heydeni* VON MEYER, 1857, by original designation.

Included species: *Planoprosopon aequus* (VON MEYER, 1857), as *Prosopon*; *P. heydeni*.

Diagnosis: Carapace longer than wide, widest at position of epibranchial region, highly dorso-ventrally compressed; rostrum axially sulcate, extending well beyond orbits; orbital concavity shallow, forward directed, bounded by at least a suborbital spine; protogastric and hepatic regions moderately defined; region between cervical and branchiocardiac grooves narrow; cervical groove deep; branchiocardiac groove moderately deep; postcervical groove moderately deep, discontinuous; carapace ornamented with large granules; sub-hepatic swelling weak; ventral extension of cervical and branchiocardiac grooves meeting to form triangular sub-epibranchial swelling.

Material examined: *Planoprosopon heydeni*, neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 36; *P. heydeni*, BSP 1957 VI 1240; SMNS 61632, SMNS 67180.

Discussion: The genus was recently diagnosed and discussed (SCHWEITZER et al. 2007); note that they originally designated *Planoprosopon* as a masculine name. Examination of a specimen of *Planoprosopon heydeni*, BM In. 28153, deposited in The Natural History Museum, London, indicates that the eye would have arisen from under the rostrum and lain in a concavity distal to the rostrum on the lateral edge of the carapace, with a small spine on the suborbital margin. This, in addition to the other diagnostic characters above, indicates that it is a member of the Longodromitidae. It is distinguished from the other genera referred to the family by its greater dorso-ventral compression, shallower orbits, and better-developed gastric regions of the carapace.

***Planoprosopon aequus* (VON MEYER, 1857) nov. comb.**

Fig. 9.1

- 1857 *Prosopon aequum* VON MEYER, 185 p. 556.
- 1860 *Prosopon aequum* – VON MEYER, p. 213, pl. 23, fig. 29.
- 1929 *N. [Nodoprosopon] Heydeni* (V. MEYER) var. *aequa* V. MEYER, 1860 – GLAESSNER, p. 271.
- 1933 *N. [Nodoprosopon] Heydeni* var. *aequa* (V. MEY.) – GLAESSNER, p. 180.

Discussion: The type material is reported to have been lost (WEHNER 1988). WEHNER (1988) considered this species to be synonymous with *Prosopon heydeni* VON MEYER, 1857 (Figs. 9.2-9.4), and indeed, the two species are very similar as illustrated by VON MEYER (1860: pl. 23) and were collected from the same locality, the Oerlinger Thals near Ulm, Germany. However, because the original type material for both species has been lost, we elect to maintain the two species as separate within the same genus, *Planoprosopon*. It appears from VON MEYER's illustrations that *P. aequus* may be somewhat shorter than *P. heydeni*, which is much longer than wide. Wehner (1988) indicated that some localities in Germany contained a shorter form of *P. heydeni*; it may be that these specimens may be referable to *P. aequus* (G. Schweigert, personal communication, January, 2008).

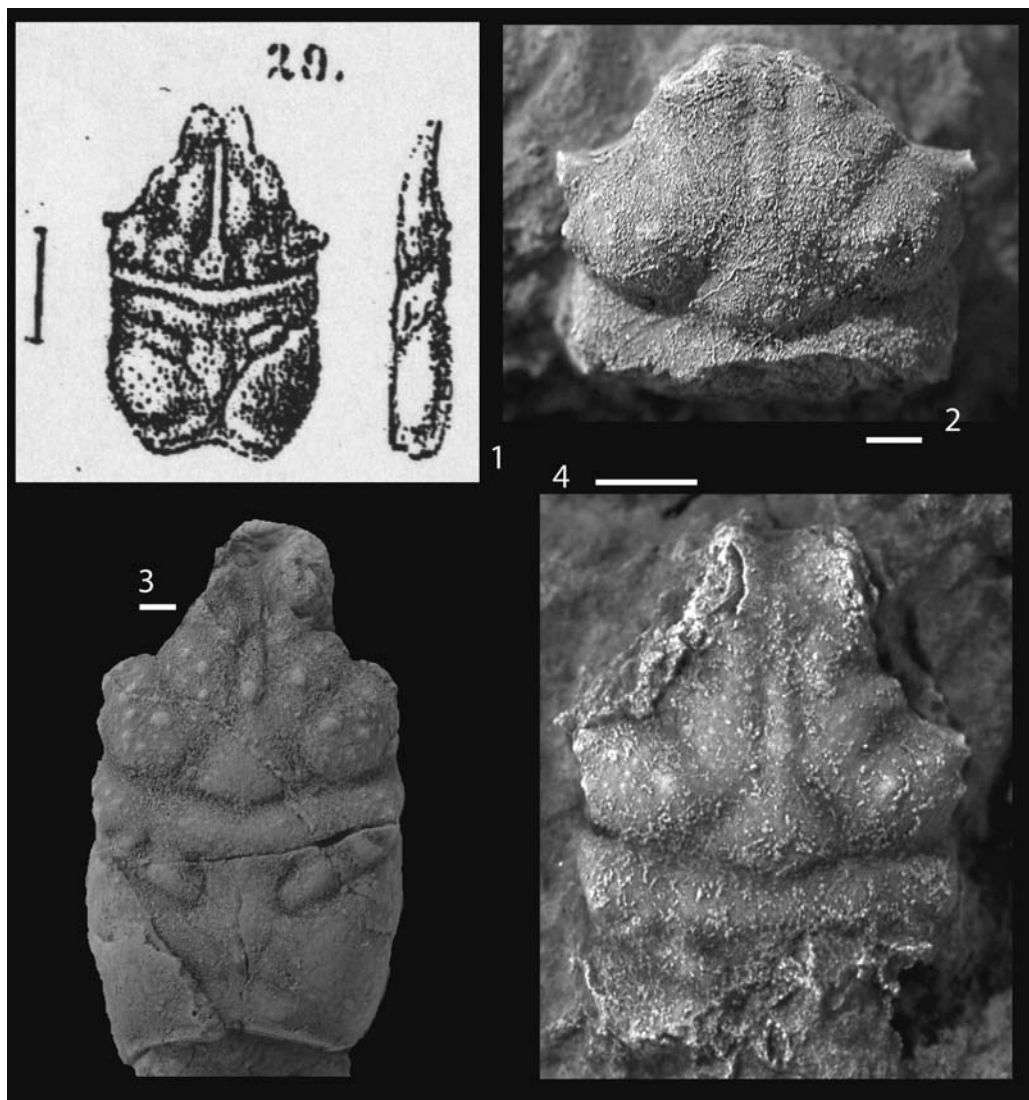


Fig. 9. *Planoprosopon* spp. 1, *Planoprosopon aequus*, digital image from VON MEYER (1860: pl. 23, fig. 29); 2, *P. heydeni*, LPBIIIart0149, Gura Dobrogei, Romania, Oxfordian (Upper Jurassic); 3, *P. heydeni*, cast of neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 36, Oerlingen bei Ulm, Germany, Upper Jurassic; 4, *P. heydeni*, LPBIIIart0148, Gura Dobrogei, Romania, Oxfordian (Upper Jurassic). Scale bars = 1 mm. Scale bar in VON MEYER illustration is of unknown length, but possibly indicates original size of fossil.

## Family Nodoprosopidae nov. fam.

Fig. 10

Included genera: *Nodoprosopon* BEURLÉN, 1928; the gender is neuter.

**Diagnosis:** Carapace longer than wide, markedly vaulted transversely, moderately so longitudinally; widest at position of mid-branchial region, about 75 percent the distance posteriorly, narrowing markedly anteriorly; rostrum trifid, with medial spine and two lateral spines that are directed upward; eyestalk apparently arising from under rostrum; orbits or augenrest not developed; lateral margins spinose; protogastric and hepatic region differentiated; carapace regions ornamented with large tubercles; cervical groove deep; postcervical groove deep, continuous across axis, extending a short distance laterally; branchiocardiac groove oriented obliquely posteriorly, deep; cardiac region small; posterior margin rimmed, broadly concave; carapace apparently with inflated subhepatic region.

**Material examined:** *Nodoprosopon ornatum* (VON MEYER, 1842) (type species), neotype, Museum Tübingen, QUENSTEDT, Jura, 1857, pl. 95, fig. 37; BSP AS III 317, original specimen of MOERICKE (1897); NHMW 1990/0041/1058, NHMW 1990/0041/2482, NHMW 1990/0041/3160, NHMW 1990/0041/3513, NHMW 1990/0041/4052, NHMW 2007/0149/0010, NHMW 2007z0162/0002.

**Occurrence:** The newly referred material was collected from the Ernstbrunn quarry localities except one specimen, NHMW 2007z0162/0002, which is from the Štramberk locality.

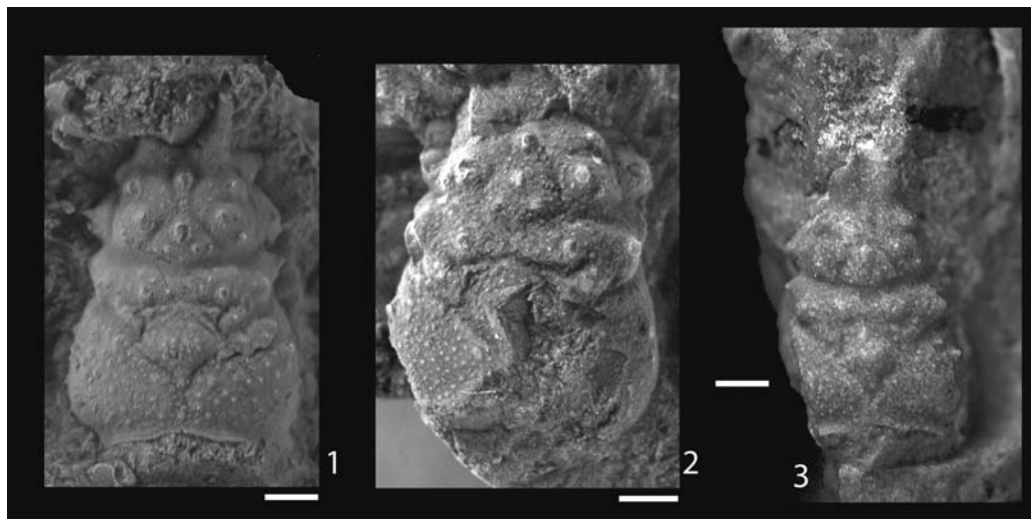


Fig. 10. Nodoprosopidae new family. 1, *Nodoprosopon ornatum*, NHMW 1990/0041/2482, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 2, *N. ornatum*, NHMW 2007/0149/0010, near Dörfles, Vienna, Ernstbrunn Limestone, Tithonian (Upper Jurassic); 3, *N. ornatum*, original specimen of MOERICKE (1897), AS III 317, Štramberk Limestone, Czech Republic, Tithonian (Upper Jurassic). Scale bars = 1 mm.



**Discussion:** The specimens of *Nodoprosopon ornatum*, the sole species thus far known, are not well preserved or are preserved surrounded by calcite geodes such that they are impossible to prepare further. Thus, some of the details of the dorsal carapace are unknown. It appears that the subhepatic area of the carapace is inflated and that this might form some aspect of an orbital area, but thus far, there is no means of testing this hypothesis. There are certainly no obvious orbital structures in members of the family. In addition, the carapace shape and the rostral shape in *Nodoprosopon* are unique among Jurassic brachyurans. Members of the Prosopidae have well-developed orbital areas to house the eyestalks, and members of the Longodromitidae possess forward-directed orbits ornamented with spines to protect the eye. Neither of these two families possesses members with dorsal carapace shapes that narrow so markedly anteriorly, nor do members have spine-like trifid rostra. Thus, the Nodoprosopidae is a well-constrained family. Its placement within the Glaessneropsoidea is somewhat problematic because it lacks orbital structures. However, this may be due to preservational bias. One exceptionally well-preserved specimen from the Ernstbrunn localities has a geode of calcite crystals surrounding the area of the carapace where the orbits would be situated. Preparation of the area would ruin the otherwise exquisite preservation of two of the rostral spines. Thus, the disposition of the orbits, if any, in this taxon remains unknown. It seems most prudent at this time to place the Nodoprosopidae within the Glaessneropsoidea, rather than to name a new superfamily for it, until better-preserved material is recovered. It seems certain that *Nodoprosopon* lacks augenrests; thus, Glaessneropsoidea is the best placement for it for now.

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### References

- ALCOCK, A. (1900): Materials for a carcinological fauna of India, 5: The Brachyura Primigenia or Dromiacea. – *Journal of the Asiatic Society of Bengal*, **68** (II/3): 123-169.
- BACHMAYER, F. (1947): Die Crustaceen aus dem Ernstbrunner Kalk der Jura-Klippenzone zwischen Donau und Thaya. – *Jahrbuch der Geologischen Bundesanstalt*, **90**: 35-47.
- (1948): Pathogene Wucherungen bei jurassischen Dekapoden. – *Sitzungsberichte der Österreich Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abt. I*, **157**: 6-10.
- (1955): Die fossilen Asseln aus den Oberjuraschichten von Ernstbrunn in Niederösterreich und von Stramberg in Mähren. – *Sitzungsberichte der Österreichische Akademie der Wissenschaften, Mathematische-naturwissenschaftliche Klasse, Abt. I*, **164**/4: 255-273.
- BEURLEN, K. (1925): Über Brachyuren- und Anomurenreste des Schwäbischen Jura. – *Neues Jahrbuch für Mineralogie Beilageband* **52/3**: 464-532, 2 figs.
- (1928): Die fossilen Dromiaceen und ihre Stammesgeschichte. – *Paläontologische Zeitschrift*, **10**: 144-183, figs. 1-7.
- (1932): Brachyurenreste aus dem Lias von Bornholm mit Beiträgen zur Phylogenie und Systematik der Brachyuren Dekapoden. – *Paläontologische Zeitschrift*, **14**: 52-66.
- COLLINS, J.S.H. & WIERZBOWSKI, A. (1985): Crabs from the Oxfordian sponge megafacies of Poland. – *Acta Geologica Polonica*, **35**/1-2: 73-88.
- COLLINS, J.S.H., ROSS, A.J., GENZANO, G. & MIANZAN, H. (2006): *Earleria* gen. nov. & *Gabriella* gen. nov., replacement names for *Foersteria* ARAI & BRINCKMANN-VOSS, 1980 (Cnidaria, Hydrozoa, Mitrocomidae) and *Foersteria* WEHNER, 1988 (Crustacea, Decapoda, Prosopidae), junior homonyms of *Foersteria* SZÉPLIGETI, 1896 (Insecta, Hymenoptera, Braconidae). – *Bulletin of the Mizunami Fossil Museum*, **33**: 125-126.
- ELIÁŠ, M. (1992): Sedimentology of the Klentice Formation and the Ernstbrunn Limestone (Ždánice-Subsilesian unit of the Outer West Carpathians). – *Věstník Českého geologického ústavu*, **67**/3: 179-193.
- ELIÁŠOVÁ, H. (1981): The Tithonian Reef of Štramberk Limestone (Czechoslovakia, West Carpathians). – *Časopis pro Mineralogii a Geologii*, **26**: 113-124, 4 pls.
- (1990): Coraux des calcaires d'Ernstbrunn (Jurassique supérieur-Crétacé-inférieur dans les Carpates externes, zone de Waschberg, Tchécoslovaquie). – *Časopis pro Mineralogii a Geologii*, **35**: 113-133.
- EUDES-DESLONGCHAMPS, J.A. (1835): Mémoire pour servir à l'histoire naturelle des Crustacés fossiles. – *Mémoire de la Société Linnéenne de Normandie*, **5**: 37-46, pl. 1.
- FELDMANN, R.M. & SCHWEITZER, C.E. (2007): Sexual dimorphism in extinct and extant Raninidae (Decapoda: Brachyura).—*Annals of Carnegie Museum*, **76**: 39-52.
- FELDMANN, R.M., LAZĂR, I. & SCHWEITZER, C.E. (2006): New crabs (Decapoda: Brachyura: Prosopidae) from Jurassic (Oxfordian) sponge bioherms of Dobrogea, Romania. – *Bulletin of the Mizunami Fossil Museum*, **33**: 1-20.

- FÖRSTER, R. (1969): Epökie, Entökie, Parasitismus und Regeneration bei fossilen Dekapoden. – *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **9**: 45-59, pls. 2, 3.
- (1985): Frühe Anomuren und Brachyuren (Decapoda, Crustacea) aus dem mittleren Dogger.—*Mitteilungen der Bayerische Staatssammlung für Paläontologie und historische Geologie*, **25**: 45-60.
- GARTH, J.S. (1973): New taxa of brachyuran crabs from deep waters off western Peru and Costa Rica.—*Bulletin of the Southern California Academy of Sciences*, **72**: 1-12.
- GLAESSNER, M.F. (1929): Crustacea Decapoda. – In: POMPECKJ, J.F. (Ed.): *Fossilium Catalogus: Animalia*, pars **41**:1-464; Berlin (W. Junk).
- (1933): Die Krabben der Juraformation. – *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abtheilung B*: 178-191.
- (1969): Decapoda. – In: MOORE, R.C. (Ed.): *Treatise on Invertebrate Paleontology*, Pt. **R4**(2): R400-R533, R626-628; Boulder and Lawrence (Geological Society of America and University of Kansas Press).
- GUINOT, D. (1978): Principes d'une classification évolutive des Crustacés Décapodes Brachyours. – *Bulletin biologique de la France et de la Belgique*, **112**(3): 211-292.
- GUINOT, D., & RICHER DE FORGES, B. (1995): Crustacea Decapoda Brachyura: Révision de la famille des Homolidae DE HAAN, 1839. In: CROSNIER, A. (ed.), *Résultats des campagnes MUSORSTOM*, Volume 13. *Mémoires du Museum National d'Histoire Naturelle*, **163**: 283-517.
- HAAN, W. DE (1833-1850): Crustacea. In: DE SIEBOLD, P.F. (ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823 – 1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit. J. Müller et Co., Lugduni-Batavorum (=Leiden)*. i-xvii, i-xxxii, ix-xvi, pp. 1-243, pls. A-J, L-Q, tab. 2.
- HÉE, A. (1924): Catalogue critique des Crustacés jurassiques du Calvados et de l'Orne. – *Bulletin de la Société Linéenne de Normandie*, **6**: 126-157, pls. 3-6.
- HOFMANN, T. (1993): Jurassic of the Eastern Alps. –In: HÖFLING, R., MOUSSAVIAN, E. & PILLER, W. (Eds): *Facial development of algae-bearing carbonate sequences in the Eastern Alps. Alpine Algae '93, International Symposium, Munich-Vienna, 29<sup>th</sup> August-5<sup>th</sup> September, Field Trip Guidebook*, pp. 1-14.
- HOUŠA, V. (1975): Geology and paleontology of the Stramberg Limestone (upper Tithonian) and the associated lower Cretaceous beds.—*Mémoires du Bureau de Recherches Géologiques et Minières*, **86**: 342-349.
- ILYIN, I.V. (2005): Cretaceous and Paleogene decapod crustaceans of the western part of Northern Eurasia. Moscow State University Press, 296 pp. (in Russian)
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. (1999): *International Code of Zoological Nomenclature*. The International Trust for Zoological Nomenclature, London, 306 pp.
- KROBICKI, M., MÜLLER, P. & ZATOŃ, M. (2007): Middle and Upper Jurassic European prosopid crabs, phylogeny and palaeoenvironments. – *Mémorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **35**: 66-67.
- KUHN, O. (1936): Neue Decapoden aus dem fränkischen Jura. – *Zentralblatt für Mineralogie, Geologie, und Paläontologie, Abt. B3*, 1936: 120-128, 10 pls.

- MARTIN, J.W. (1990): Crabs of the family Homolodromiidae, II. *Dicranodromia felderi*, new species, from the western Atlantic, with notes on the type series of *D. ovata* A. MILNE EDWARDS, 1880. – *Journal of Crustacean Biology*, **10**: 708-720.
- MARTIN, J.W. & DAVIS, G.B. (2001): An updated classification of the recent Crustacea. – *Natural History Museum of Los Angeles County, Science Series* **39**: 1-124.
- VON MEYER, H. (1835): Briefliche Mittheilungen. – *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, p. 329.
- (1840): Neue Gattungen fossiler Krebse aus Gebilden vom bunten Sandsteine bis in die Kreide.—1-23; Stuttgart (E. Schweizerbart).
- (1842): Über die in dem dichten Jurakalk von Aalen in Württemberg vorkommenden Spezies des Crustaceengenus *Prosopon*. – *Beiträge zur Petrefaktenkunde*, Heft **5**: 70-75, pl. 15.
- (1856): Briefliche Mittheilungen. – *Jahrbuch für Mineralogie, Geologie, und Paläontologie*, p. 51.
- (1857): Briefliche Mittheilungen. – *Jahrbuch für Mineralogie, Geologie, und Paläontologie*, p. 556.
- (1858): Briefliche Mittheilungen. – *Jahrbuch für Mineralogie, Geologie, und Paläontologie*, p. 59-62
- (1860): Die Prosoponiden oder die Familie der Maskenkrebse. – *Palaeontographica*, **7**: 183-222, pl. 23.
- MOERICKE, W. (1897): Die Crustaceen der Stramberger Schichten. – *Palaeontographica*, Supplement II, Sechste Abtheilung: 43-72, pl. 6.
- MORRIS, S.G. (1980): Catalogue of the type and figured specimens of fossil Crustacea (excl. Ostracoda), Chelicerata, Myriapoda and Pycnogonida in the British Museum (Natural History). – *Trustees of the British Museum (Natural History)*, 53 pp., 3 pls.
- MÜLLER, P., KROBICKI, M. & WEHNER, G. (2000): Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) – their taxonomy, ecology and biogeography. – *Annales Societatis Geologorum Poloniae*, **70**: 49-79.
- MUȚIU, R. & BĂDĂLUȚĂ, A. (1971): La présence des décapodes anomures et dromiacés dans les calcaires tithoniques de Plate-Forme Moëssienne. – *Annales Institutii Geologici Publici Hungarici*, **54** (2): 245-525, pl. 1.
- ORTMANN, A.E. (1892): Die Decapoden-Krebse des Strassburger Museums. Theil 5, Die Abtheilungen Hippidea, Dromiidae und Oxystomata. – *Zoologische Jahrbücher, Abtheilung für Systematik*, **6**: 532-588, pl. 26.
- PATRULIUS, D. (1959): Contributions à la systématique des décapodes néojurassiques. – *Revue de Géologie et Géographie*, **3**(2): 249-257.
- (1966): Les décapodes du Tithonique inférieur de Woźniki (Carpates Polonaises Occidentales). – *Annales de la Société Géologique de Pologne*, **36**: 495-517, pls. 30, 31.
- QUENSTEDT, F.A. (1856-1857): *Der Jura*. – 842 pp., 100 pls; Tübingen (Verlag der H. Lauppischen Buchhandlung).
- (1867): *Handbuch der Petrefaktenkunde*, 2<sup>nd</sup> edition. – 982 pp., 1 Atlas with 86 pls.; Tübingen (H. Laupp).
- REUSS, A.E. (1858 [imprint 1857]): Über kurzschwänzige Krebse im Jurakalke Mährens. – *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, **31** : 5-13.

- (1859): Zur Kenntnis fossiler Krabben. – Akademie der Wissenschaften Wien, Denkschrift **17**: 1-90, pls. 1-24.
- REMEŠ, M. (1895): Beiträge zur Kenntnis der Crustaceen der Stramberger Schichten.- Bulletin International de l'Académie des Sciences de Bohème (Prague), **2**: 200-204, pls. 1-3.
- SAMOUELLE, G. (1819): The entomologist's useful compendium, or an introduction to the knowledge of British insects. T. Boys, London, 486 pp., 12 pls.
- SCHWEIGERT, G. (2006): A specimen of *Prosopon hebes* v. MEYER, 1840 (Decapoda: Brachyura: Prosopidae) from the Middle Jurassic of SW Germany. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 2006(6): 361-370.
- SCHWEITZER, C.E. & FELDMANN, R.M. (2008 [imprint 2007]): A new classification for some Jurassic Brachyura (Crustacea: Decapoda: Brachyura: Homolodromioidea): Families Goniodromitidae BEURLIN, 1932 and Tanidromitidae new family. – Senckenbergiana lethaea, **87**(2): 119-156.
- SCHWEITZER, C.E., FELDMANN, R.M. & LAZĂR, I. (2007): Decapods from Jurassic (Oxfordian) sponge megafacies of Dobrogea, Romania and reconsideration of *Nodoprosopon* BEURLIN, 1928. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **244**: 99-113.
- SCHWEITZER, C.E., NYBORG, T.G., FELDMANN, R.M. & ROSS, R.L.M. (2004): Homolidae DE HAAN, 1839 and Homolodromiidae ALCOCK, 1900 (Crustacea: Decapoda: Brachyura) from the Pacific Northwest of North America and a reassessment of their fossil record.— Journal of Paleontology, **78**: 133-149.
- STOLLEY, E. (1924): Über einige Krebsreste aus schweizerischem und norddeutschem Neokom. – Eclogae Geologicae Helvetiae, **18**: 411-429, pl. 13.
- VAN STRAELEN, V. (1924[imprint 1925]): Contribution à l'étude des crustacés décapodes de la période jurassique. – Mémoires d'Académie Royale de Belgique, Cl. Sci., collected in number 4, series 2, **7**: 1-462, pls. 1-10.
- (1936): Crustacés Décapodes nouveaux ou peu connus de l'époque Crétacique. – Bulletin du Museum Royale d'Histoire Naturelle de Belgique, **12/** 45: 50 pp., 4 pls.
- WEHNER, G. (1988): Über die Prosoponiden (Crustacea, Decapoda) des Jura.- 154 pp., 8 pls., 1 insert; Dissertation zur Erlangung des Doktorgrades der Fakultät für Geowissenschaften der Ludwig-Maximilians-Universität zu München.
- WITHERS, T.H. (1951): Some Jurassic and Cretaceous crabs (Prosoponidae). – Bulletin of the British Museum (Natural History), Geology, **1**(6): 171-186, pls. 15-17.
- WOODWARD, H. (1865): On the oldest known British Crab (*Palaeinachus longipes*) from the forest marble of Malmesbury, Wilts. – Quarterly Journal of the Geological Society, **22**: 493-494, pl. 14.
- (1868): On a new brachyurous Crustacean (*Prosopon mammillatum*) from the Great Oolite, Stonesfield. – Geological Magazine, **5**: 3-5, pl. 1.
- WRIGHT, C.W. & COLLINS, J.S.H. (1972): British Cretaceous Crabs. – Palaeontographical Society Monographs, **126/533**: 1-113.
- ZEISS, A. (2001): Die Ammonitenfauna der Tithonklippen von Ernstbrunn, Niederösterreich. – Neue Denkschriften des Naturhistorischen Museums in Wien, **6**: 1-116.



