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JURASSIC AND CRETACEOUS PRIMITIVE CRABS OF THE FAMILY PROSOPIDAE (DECAPODA: BRACHYURA) – THEIR TAXONOMY, ECOLOGY AND BIOGEOGRAPHY

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Abstract: The Prosopidae is an extinct family, consisting mostly of Mesozoic species. Most probably it accommodates the ancestors of all brachyurans in the large sense. The family appeared in the Late Pliensbachian and disappeared at the Early Palaeocene.

Evolution of the Prosopidae, and therefore, brachyuran evolution started on Middle Jurassic, shallow, soft bottom marine environments. The world-wide Callovian transgression made possible the formation of bioherms and reefs in the Late Jurassic, creating ecological niches for the rapidly differentiating prosopids. These crabs migrated rapidly all over Europe in the Oxfordian and began to flourish and massively occupied sponge megafacies from Portugal to Poland. In the Kimmeridgian, the area of known prosopids shrank, which has probably been connected with decreasing of the reef facies. In turn, a Tithonian regression in the peri-Tethyan area resulted in changes of habitats and in colonisation of the coral reefs.

When reef facies retreated at the Jurassic–Cretaceous boundary, the favourable conditions for crab development also vanished, so the known Cretaceous prosopids are rare and spatially dispersed. In Tertiary, the closely related descendants of them, homolodromiids, inhabited preferably soft muddy bottoms in deeper, colder waters.

Abstrakt: Kraby z rodziny Prosopidae, reprezentowane są prawie wyłącznie przez gatunki mezozoiczne. Z filogenetycznego punktu widzenia, są one prawdopodobnie przodkami wszystkich pozostałych gatunków krabów. Przedstawiciele tej rodziny znani są od późnego pliensbachu do wczesnego paleocenu.

Ewolucja prosopidów, a poprzez to ewolucja pozostałych krabów, rozpoczęła sią w środkowojurajskich, płytkich środowiskach morskich o miękkim charakterze dna. Ogólnoświatowa transgresja kelowejska stworzyła dogodne warunki do powstania różnorodnych bioherm i raf w późnej jurze, które stanowiły nisze ekologiczne dla szybko różnicujących się dzięki temu krabów z rodziny Prosopidae. Kraby te migrowały gwałtownie na całą Europę w oksfordzie, masowo zasiedlając megafację gąbkową i są obecnie znajdowane w utworach tej facji od Portugalii do Polski. W kimerydzie obszar występowania prosopidów wyraźnie się skurczył, co było prawdopodobnie związane ze stopniowym zanikiem tej facji. Z kolei w tytonie regresja w obszarach perytetydzkich spowodowała zmianę środowiska życia krabów i kolonizację przez nie raf koralowych.

Dogodne warunki dla rozwoju tych krabów gwałtownie się pogorszyły blisko granicy jury i kredy (zanikanie facji rafowych) skutkiem czego kredowe prosopidy są rzadkie i geograficznie rozproszone. W trzeciorzędzie najbliżsi potomkowie rodziny Prosopidae – kopalni przedstawiciele rodziny Homolodromiidae – zasiedlili środowiska miękkich den głębszych i zimniejszych mórz.

Key words: Decapoda, family Prosopidae, Jurassic, Cretaceous, taxonomy, palaeoecology, palaeobiogeography.

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INTRODUCTION

by P. Müller

The Prosopidae von Meyer, 1860 is an extinct family, which belongs to Dromiacea, the most primitive crabs, consisting mostly of Mesozoic species. Most probably it accommodates the ancestors of all brachyurans in the broad sense. The species are almost exclusively known by their carapace. Limbs or ventral parts very seldom occur with carapaces. The carapace is dromiid-like in many respects, generally elongate but rarely subcircular or subtriangular in outline, and moderately or rather strongly convex transversally. Cervical and branchiocardiac grooves are invariably present, generally quite deep. Ornamentation may be quite strong, but sometimes the carapace is almost smooth, except for the mentioned grooves. Lateral margins are absent or partly developed. Orbital depressions generally appear as elongate grooves, but may be completely absent.

The family Prosopidae appeared in the late Early Jurassic (Fig. 1); one genus survived the Cretaceous/Tertiary boundary but disappeared at the end of the Danian, Early Palaeocene age. If accepting the view of Wright & Collins (1972) in placing *Noetlingia* into the Prosopidae, the record of the family would last to the Early Oligocene. However, this genus may represent an aberrant dromiid. Fossil evidence (Glaessner, 1969) suggests that the family Prosopidae

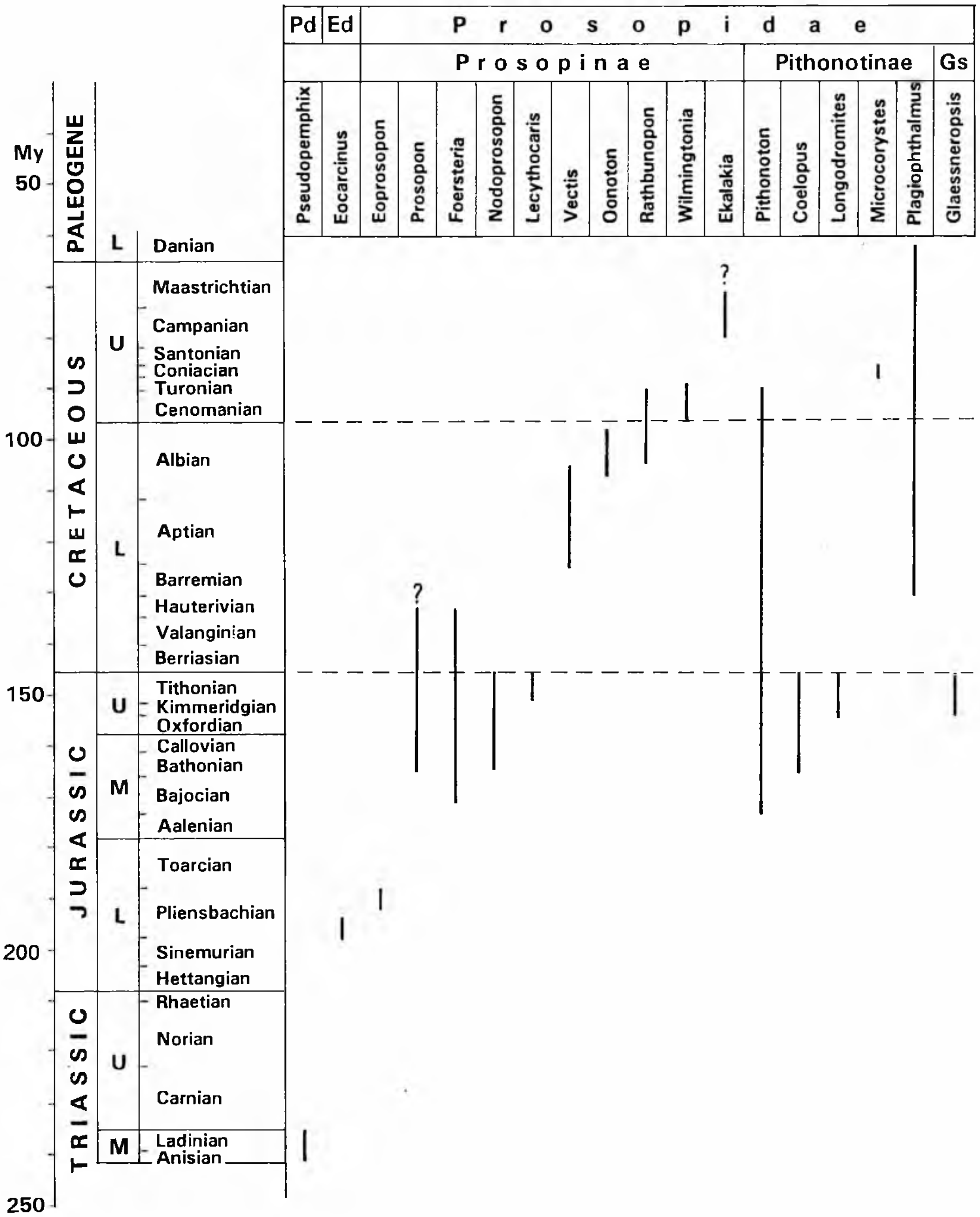

Fig. 1. Stratigraphical ranges of genera from families Prosopidae, Pemphicidae (Pd) and Eocarcinidae (Ed); Gs – subfamily Glaessneropsinae

is ancestral to all other brachyurans in the broad, classical sense, including Dromiacea and Eubrachyura.

Meyer (1842, 1860) was the first to report on prosopids. Recognising their dromiid affinities, he arranged the 25 known species into a separate, new family. Except for one galatheid species, *Gastrosacus wetzleri* von Meyer, his forms are still regarded as belonging to the Prosopidae. A set of taxonomic works subsequently appeared considerably elevating the number of species (Remeš, 1895; Moericke, 1889; Blaschke, 1911). Beurlen (1928b, 1933) described the "explosiven Formenbildung", arguing for an early branching of Brachyura. He suggested that ancestors of most extant crabs may be identified among early members of the family Prosopidae. His views, based partly on erroneous stratigraphic data, were discussed by Glaessner (1933). In succeeding contributions (e.g., Patrulius, 1960, 1966; Collins & Wierzbowski, 1985), the new taxa have been described, being helpful in understanding stratigraphic distribution and ecology of the family.

Withers (1932) described an Early Jurassic decapod, *Eocarcinus praecursor* Withers, and interpreted it as a transitional form between macrurous decapods and crabs. Förster (1986) recognised one more transitional form (*Eoprosopon klugi* Förster) between *Eocarcinus* and later prosopids. Wright & Collins (1972) and Wehner (1988) gave monographic accounts of prosopids from the Cretaceous and the Jurassic respectively.

SYSTEMATIC PALAEONTOLOGY

by P. Müller

Subsection DROMIACEA de Haan, 1833
Superfamily HOMOLODROMIOIDEA Alcock, 1899
Family PROSOPIDAE von Meyer, 1860

Diagnosis: The family is almost exclusively known by isolated carapaces; in a few cases, ventral, abdominal parts and somites of limbs are also preserved. Carapace is subcylindrical or may be flattened, subcircular or triangular, and is small. The largest Jurassic form, *Pithonoton grande* (von Meyer) hardly exceeds 30 mm, while some Cretaceous species may have been slightly larger. Sharp lateral margins are absent or incomplete. Elongate to almost circular orbital grooves are present or absent. In the few examples, where preserved, the chelae of first pereiopods are *Homolodromia*-like (Meyer, 1860; Förster, 1985b). Cervical and branchiocardiac grooves are well developed, postcervical groove is strongly reduced or absent. Rounded triangular telson and the 2nd to 6th abdominal somites are visible on the indeterminable specimen from the Middle Jurassic (Fig. 2) (Förster, 1985b).

Remarks: All described features make prosopids similar to *Homolodromia* to such an extent that Glaessner (1969) assigned Homolodromiinae into the family Prosopidae.

Distribution: Europe, Africa, North America, Asia, Australia, Antarctica; Early Jurassic (Pliensbachian) to Paleocene (Danian).

Subfamily PROSOPINAE von Meyer, 1860

Diagnosis: Carapace generally elongate, subcylindrical, without sharp lateral margin, projecting rostrum of moderate size, orbital grooves absent or rudimentary.

Distribution: Europe, Africa, North America, Australia; Pliensbachian to Campanian.

Genus *Eoprosopon* Förster, 1986
Type species: *Eoprosopon klugi* Förster, 1986
Fig. 3

Diagnosis: Carapace elongate, dorsoventrally flattened; cervical furrow deep; branchiocardiac shallow; gastric region strongly subdivided. First pair of pereiopods chelate, with chelae elongate. Upper crest and external surface dentate. Fourth and fifth pereiopods reduced, upturned dorsally.

Remarks: Only one species, *Eoprosopon klugi* Förster, 1986 (Fig. 3) has been distinguished within this genus.

Distribution: Europe; Pliensbachian.

Genus *Prosopon* von Meyer, 1835
Type species: *Prosopon tuberosum* von Meyer, 1840
Fig. 4; Fig. 17 A–C

Diagnosis: Carapace elongate, convex; posterior margin wide; no orbital grooves; branchiocardiac groove strong.

Remarks: Eight species have been recognised (one species as *cf.*).

Distribution: Europe; Middle Jurassic to Lower Cretaceous.

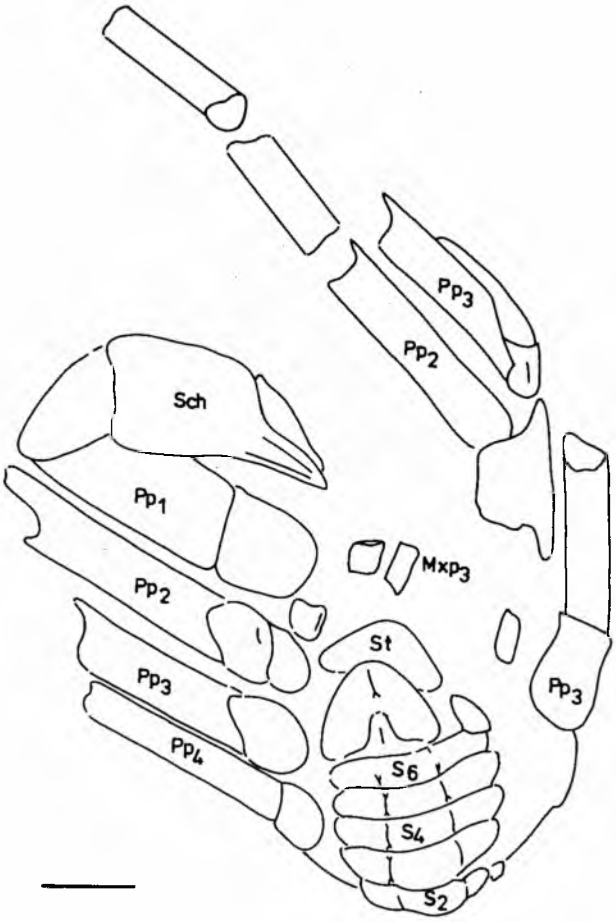

Fig. 2. Prosopidae indet.; ventral side. Upper Bajocian, Switzerland (after Förster, 1985b). Pp – proximal somite of pereiopods 1 to 4; Sch – chela of first pereiopod; St – 5th segment of sternum; S – segment of abdomen; Mxp$_3$ – remnants of 3rd maxilliped. Length of scale bar – 2 mm

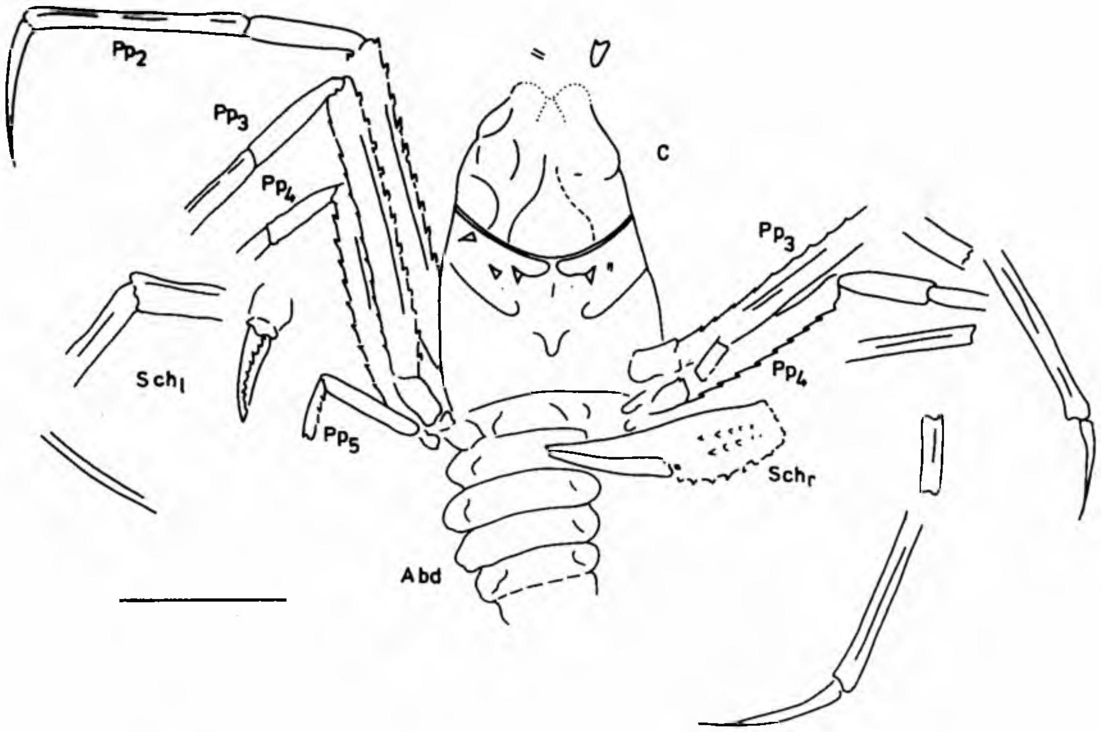

Fig. 3. *Eoprosopon klugi* Förster. Upper Pliensbachian, Tongrube Marloffstein near Erlangen (after Förster, 1986); Abd – abdomen; C – carapace; other designations as in Fig. 2. Length of scale bar – 6 mm

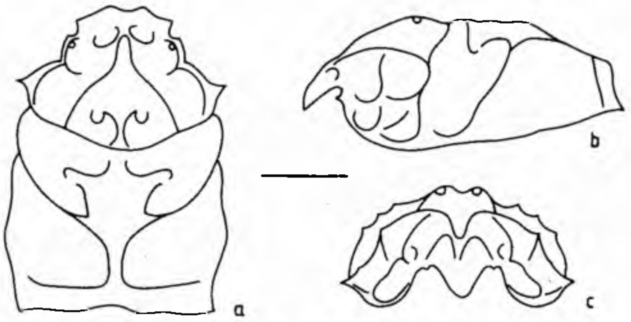

Fig. 4. *Prosopon mammillatum* Woodward. Middle Bathonian, Stonesfield, Oxfordshire (after Wehner, 1988); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 10 mm

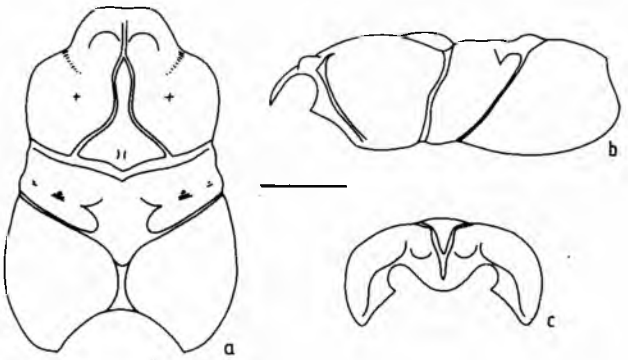

Fig. 5. *Foersteria biburgensis* Wehner. Upper Oxfordian, Biburg at Weißenburg, Bavaria (after Wehner, 1988); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 5 mm

Genus *Foersteria* Wehner, 1988

Type species: *Foersteria biburgensis* Wehner, 1988

Fig. 5; Fig. 17 D

Diagnosis: Carapace elongate; branchial region slightly swollen; semicylindrical in cross-section, without lateral margins. Surface smooth with some small protuberances; wide urogastric lobes; bilobate rostrum.

Remarks: Seven species have been recognised.

Distribution: Europe, Africa; Middle Jurassic to Lower Cretaceous.

Genus *Nodoprosopon* Beurlen, 1928

Type species: *Nodoprosopon ornatum* (von Meyer, 1860)

Fig. 6; Fig. 17 E–I

Diagnosis: Carapace elongate, quadrangular, front wide; orbital grooves delimited with a ridge or a serrated margin.

Remarks: Eight species have been recognised; four other assigned to this genus with a question mark.

Distribution: Europe; Middle and Upper Jurassic.

Genus *Lecythocaris* von Meyer, 1860

Type species: *Lecythocaris paradoxa* von Meyer, 1860

Fig. 7; Fig. 17 J

Diagnosis: Carapace broadly pentagonal, strongly areolated; branchial region swollen; large, bilobate rostrum.

Remarks: One species has been recognised.

Distribution: Europe; Upper Jurassic.

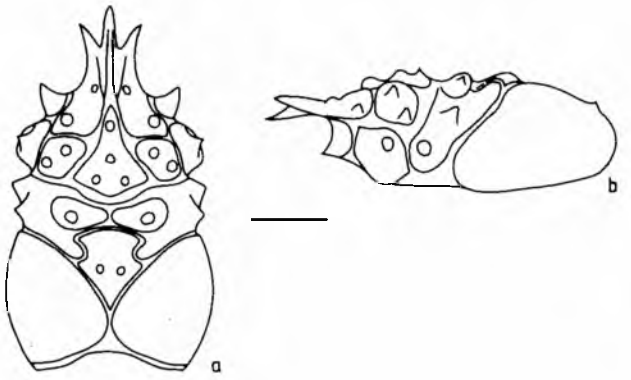

Fig. 6. *Nodoprosopon ornatum* (von Meyer). Kimmeridgian, Örlinger Tal, Baden-Würtemberg, reconstruction after several specimens (after Wehner, 1988); a – dorsal view; b – lateral view. Length of scale bar – 2 mm

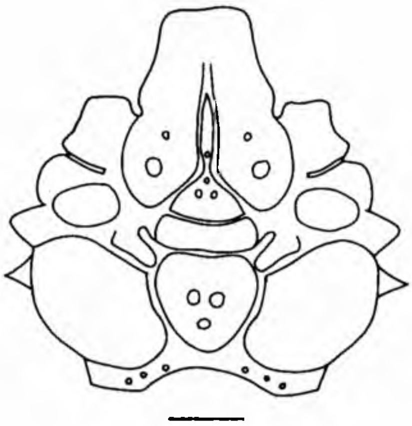

Fig. 7. *Lecythocaris paradoxa* von Meyer. Reconstruction after several specimens, Upper Jurassic, Europe (after Wehner, 1988); dorsal view. Length of scale bar – 2 mm

Genus *Vectis* Withers, 1946
Type species: *Vectis wrighti* Withers, 1946
Fig. 8

Diagnosis: Ovoid carapace, widest at the metabranchial region; distinct and tumid lobes; lateral margin marked by tubercles, deep orbital sockets.

Remarks: Three species have been recognised.

Distribution: Europe; Aptian to Albian.

Genus *Oonoton* Glaessner, 1980
Type species: *Oonoton woodsi* Glaessner, 1980

Diagnosis: Ovoid carapace, without sharp lateral margins; short posterior margin, truncated triangular rostrum with a transverse grooves; mesogastric lobe long and narrow. Carapace surface granulated.

Remarks: One species has been recognised. This genus is similar to *Vectis* but differs from it in details of shape and surface sculpture (e.g., posterior margin not as long as in *Vectis*).

Distribution: Australia; Albian.

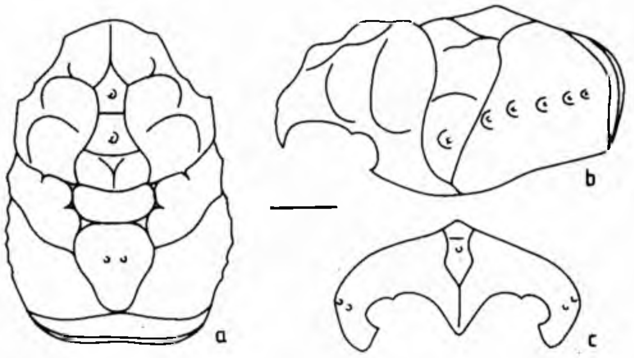

Fig. 8. *Vectis wrighti* Withers. Lower Aptian, Isle of Wight, England (after Glaessner, 1969); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 1 mm

Fig. 9. *Rathbunopon polyakron* Stenzel. Cenomanian, Travis county, Texas (after Glaessner, 1969); dorsal view. Length of scale bar – 3 mm

Genus ?*Rathbunopon* Stenzel, 1945
Type species: *Rathbunopon polyakron* Stenzel, 1945
Fig. 9

Diagnosis: Carapace ovoid to subquadrate, evenly arched in transverse section; rostrum steeply downturned, grooved triangular; orbital depression well defined; no distinct lateral margins.

Remarks: Bishop (1986a) doubts its prosopid affinity. Four species have been recognised.

Distribution: Europe, North America; Albian to Cenomanian.

Genus *Wilmingtonia* Wright & Collins, 1972
Type species: *Wilmingtonia satyrica* Wright & Collins, 1972
Fig. 10

Diagnosis: Carapace rectangular with strong areolation; blunt, downturned front; incomplete but distinct orbital grooves.

Remarks: One species has been recognised.

Distribution: Europe; Cenomanian.

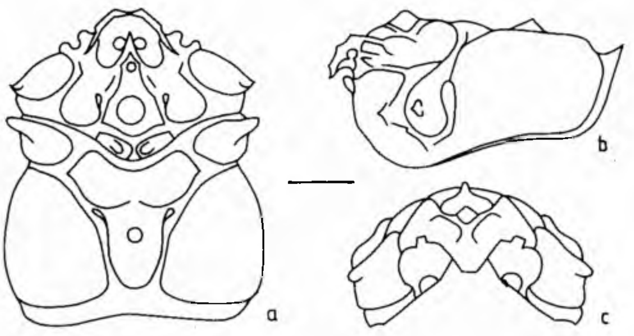

Fig. 10. *Wilmingtonia satyrica* Wright & Collins. Cenomanian, Wilmington, England (after Wright & Collins, 1972); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 10 mm

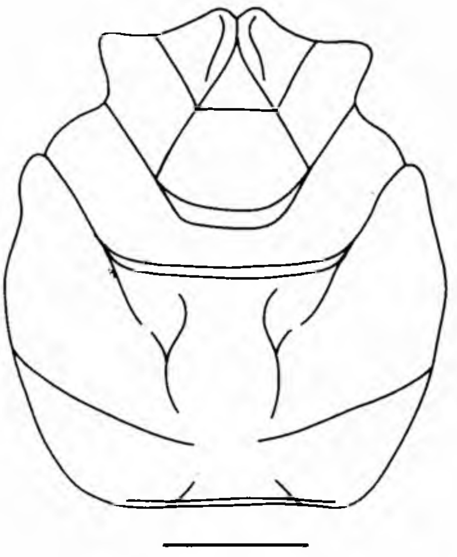

Fig. 11. *Ekalakia lamberti* Bishop. Campanian or Maastrichtian, eastern Montana, U.S.A. (after Bishop, 1976); dorsal view. Length of scale bar – 4 mm

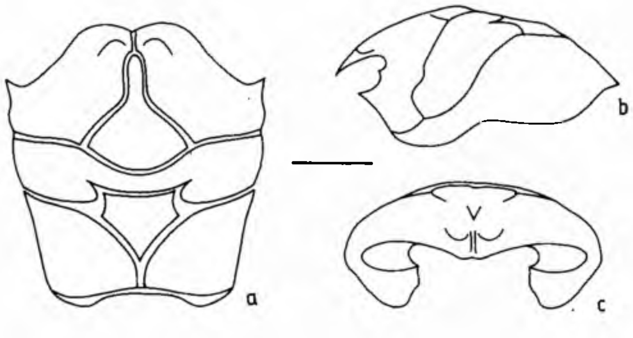

Fig. 12. *Pithonoton marginatum* (von Meyer). Reconstruction after several specimens; Kimmeridgian to Tithonian, Europe (after Wehner, 1988); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 4 mm

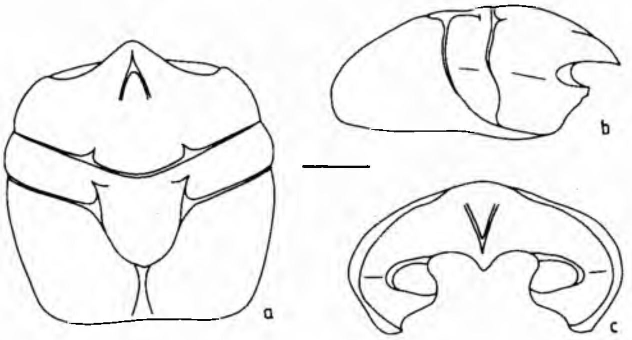

Fig. 13. *Coelopus hoheneggeri* (Moericke). Upper Tithonian, Czech Republic (after Wehner, 1988); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 2 mm

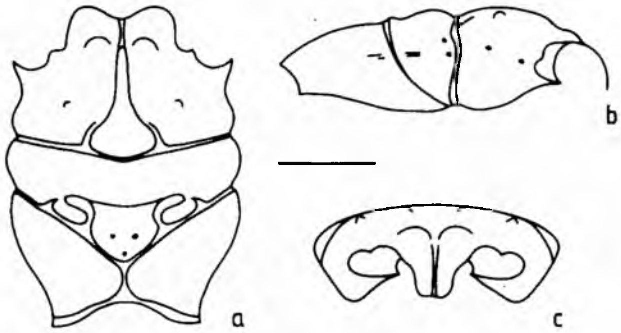

Fig. 14. *Longodromites excisus* (von Meyer). Reconstruction after several specimens; Oxfordian to Tithonian, central Europe (after Wehner, 1988); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 3 mm

Genus ?*Ekalakia* Bishop, 1976
Type species: *Ekalakia lamberti* Bishop, 1976
Fig. 11

Diagnosis: Carapace ovate, nearly circular with protruding rectangular anterior part; carapace strongly convex transversally; equally deep, subparallel, U-shaped branchiocardiac and cervical grooves; rostrum downturned with median sulcus.
Remarks: One species has been recognised.
Distribution: North America; Campanian or Maastrichtian.

Subfamily PITHONOTINAE Glaessner, 1933

Diagnosis: Carapace generally smooth; wide fronto-orbital margin, often flat or subcylindrical; lateral margins present, sometimes well developed.
Distribution: Europe, North America, Antarctica; Middle Jurassic to Paleocene (Danian).

Genus *Pithonoton* von Meyer, 1842
Type species: *Pithonoton marginatum* (von Meyer, 1842)
Fig. 12; Fig. 17 K, L; Fig. 18 A–E

Diagnosis: Carapace smooth or finely tuberculated, ovoid or subpentagonal, slightly or quite strongly convex; lateral margins present at the anterior and median parts, often quite distinct, sometimes obscure; rostrum bilobate; well delimited, orbital grooves very long.

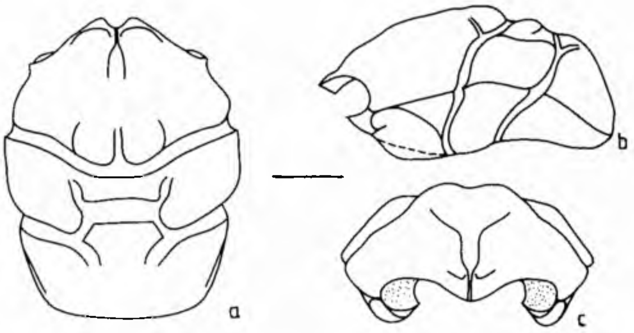

Fig. 15. *Plagiophthalmus oviformis* Bell. Cenomanian, Wilmington, England (after Wright & Collins, 1972); a – dorsal view; b – lateral view; c – frontal view. Length of scale bar – 5 mm

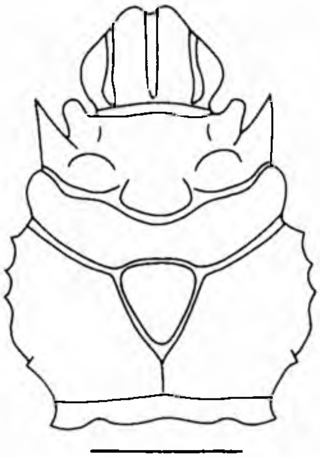

Fig. 16. *Glaessneropsis heraldica* (Moericke). Tithonian, Czech Republic (after Wehner, 1988); dorsal view. Length of scale bar – 2 mm

Remarks: This genus includes thirteen species (one designated as *cf.*).
Distribution: Europe; Middle Jurassic to Cenomanian.

Genus *Coelopus* Etallon, 1861
Type species: *Coelopus jolyi* Etallon, 1861
Fig. 13; Fig. 18 F

Diagnosis: Carapace subquadrangular, with weakly developed lateral margins at the anterior and median part; parallel branchiocardiac and cervical furrows closely placed; rostrum small, triangular; orbital grooves deep and short, well delimited; carapace smooth or finely granulated.
Remarks: Four species have been recognised.
Distribution: Europe; Middle to Upper Jurassic.

Genus *Longodromites* Patrulius, 1960
Type species: *Longodromites excisus* (von Meyer, 1857)
Fig. 14; Fig. 18 G

Diagnosis: Carapace suboval, elongate with poorly developed lateral margin; short, round orbital grooves, with small tooth on the supraorbital margin; rostrum downturned, bilobed, wide. The branchial regions triangular, delimited by curved and ridged posterior margin.
Remarks: Three species and one subspecies have been recognised.
Distribution: Europe; Upper Jurassic.

Genus ?*Microcorystes* Fritsch, 1893
Type species: *Microcorystes parvulus* Fritsch, 1893

Diagnosis: Carapace small elliptical with very large orbits, bosses raised mesogastric and cardiac.
Remarks: This genus is frequently assigned to Dromiidae. One species has been recognised.
Distribution: Europe; Coniacian.

Genus *Plagiophthalmus* Bell, 1863
Type species: *Plagiophthalmus oviformis* Bell, 1863
Fig. 15

Diagnosis: Carapace elliptical or subquadrangular, elongate, strongly convex; lateral margins well developed even behind the branchiocardiac furrow; carapaces may have spines. Branchiocardiac and cervical furrows well, subequally developed; no distinct depressions at the posterior margin for the last pereiopods.
Remarks: This is the only known prosopid surviving the Cretaceous/Tertiary boundary (we regard the Eocene–Oligocene *Noetlingia*, sometimes assigned to prosopids, as an aberrant dromiid). Six Cretaceous and one Danian species have been recognised (Segerberg, 1900; Woodward, 1901; Wright & Collins, 1972; Collins & Jakobsen, 1994; Jakobsen & Collins, 1997).
Distribution: Europe, North America, Antarctica; Barremian to Danian (Lower Palaeocene).

Subfamily GLAESSNEROPSINAE Patrulius, 1960

Diagnosis: Carapace subquadrate or elliptical, convex, ornamented, with very wide, crown-shaped rostrum; three strong orbital lobes.
Distribution: Europe; Upper Jurassic.

Genus *Glaessneropsis* Patrulius, 1960
Type species: *Glaessneropsis heraldica* (Moericke, 1889)
Fig. 16; Fig. 18 H

Diagnosis: Carapace ovoid or subrectangular, convex; branchial region slightly swollen; rostrum large, crown-shaped, three orbital lobes over the orbital grooves; cervical and branchiocardiac grooves subparallel; surface of the branchial region finely granulated.
Remarks: One species has been recognised.
Distribution: Europe; Upper Jurassic.

ORIGIN, CLOSEST RELATIVES, PROBABLE DESCENDANTS

by P. Müller

The following ancestor-descendant relationships are based only or mainly on palaeontological-morphological evidence (Fig. 19). Evidently, parallel or converging trends in morphological evolution, even in larval development, may deceive both palaeontologists and zoologists. We think it will be a task for the future to harmonise palaeontological evidences with views of zoologists, if possible based on DNA sequencing. Anyway, for the moment it is clear that palaeontology may be the only potential tool to validate evolution in real time.

Withers (1932) described the Early Jurassic *Eocarcinus*

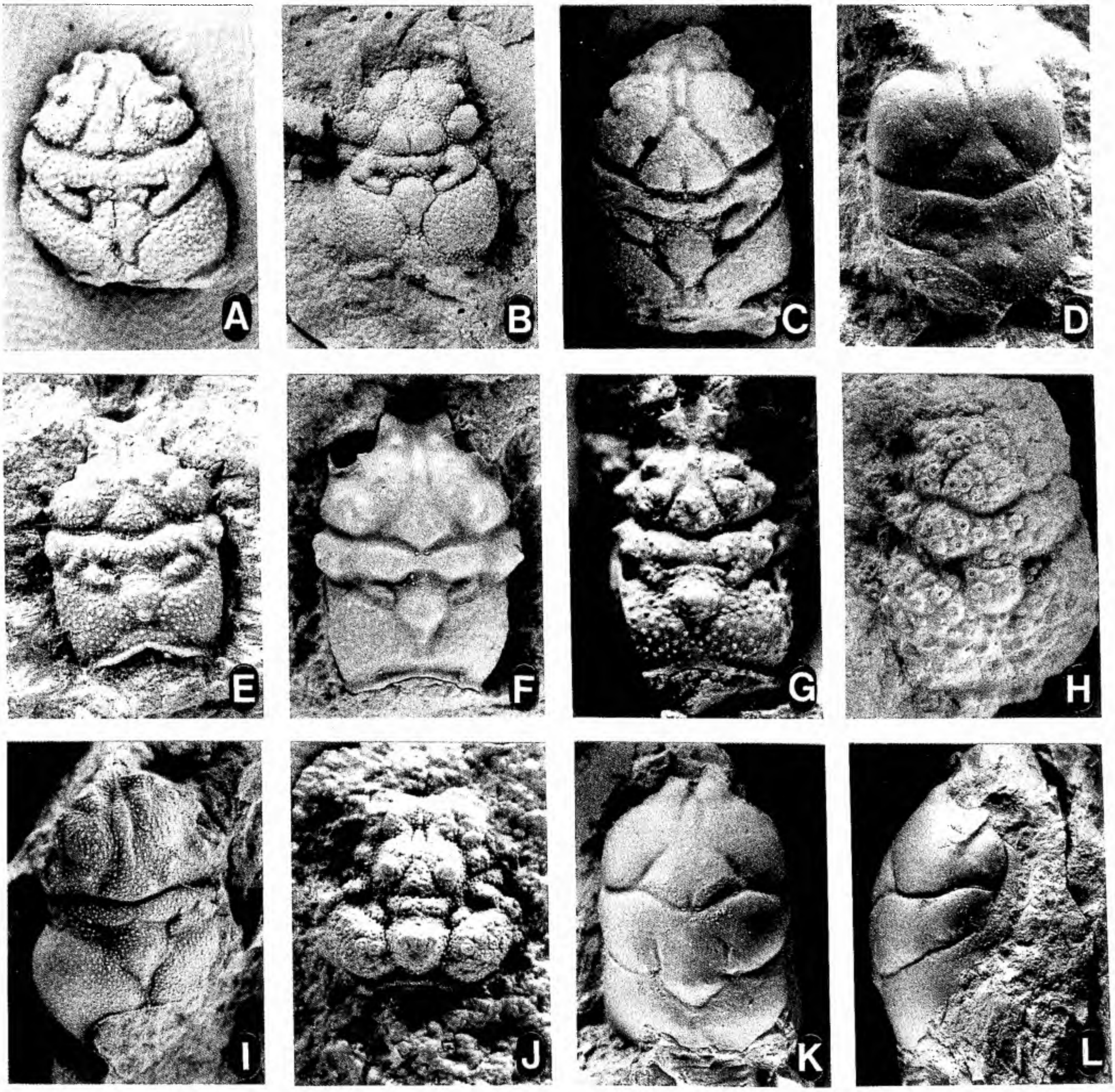

Fig. 17. Selected species of the family Prosopidae (subfamily: Prosopinae – **A-J**; Pithonotinae – **K, L**) (after Wehner, 1988). **A.** *Prosopon aculeatum* von Meyer (neotype), Malm ε, Örlinger Tal at Ulm (Germany), Museum Tübingen, carapace length (Cl) – 6 mm; **B.** *Prosopon protuberosum* Wehner (holotype – silicon cast of concave form), Malm ε, Saal at Kelheim (Germany), private collection (Sylla/Arget): Nr. 1, Cl – about 3 mm; **C.** *Prosopon punctatum* von Meyer (neotype), Tithonian, Kotzobenz (Czech Republic), Bayerische Staatssammlung für Paläontologie (Munich) (BSP): AS III 307, Cl – 12.5 mm; **D.** *Foersteria biburgensis* Wehner (holotype), Malm β, Biburg at Weißenburg (Germany), BSP: 1980 XXX 514, Cl – 8 mm; **E.** *Nodoprosopon heydeni* (von Meyer), Malm δ, Petersbuch/Michellohe (Germany), BSP: 1988 I 89, Cl – 7 mm; **F.** *Nodoprosopon spinosum* (von Meyer) (neotype), Malm β, Biburg at Weißenburg (Germany), BSP: 1988 XXX 528, Cl – 8 mm; **G.** *Nodoprosopon ornatum* (von Meyer), Tithonian, Willamowitz (Czech Republic), BSP: AS III 317, Cl – 5 mm; **H.** *Nodoprosopon torosum* (von Meyer), Malm β, Raitenbach/Gersdorf (Germany), BSP: 1962 I 528, Cl – 13 mm; **I.** *Nodoprosopon mirum* (Moericke), isopod-infected specimen, Malm δ, Geislingen at Steige (Germany), Staatliches Museum für Naturkunde (Stuttgart) (SMNS): 61671, Cl – 15 mm; **J.** *Lecythocaris paradoxa* von Meyer (neotype – silicon cast of concave form), Malm ε, Örlinger Tal at Ulm (Germany), Museum Tübingen, Cl – 5 mm; **K, L.** *Pithonoton insigne* (von Meyer) (K – dorsal view, L – lateral view), Malm δ, Nusplingen (Germany), SMNS: 61666, Cl – 16 mm

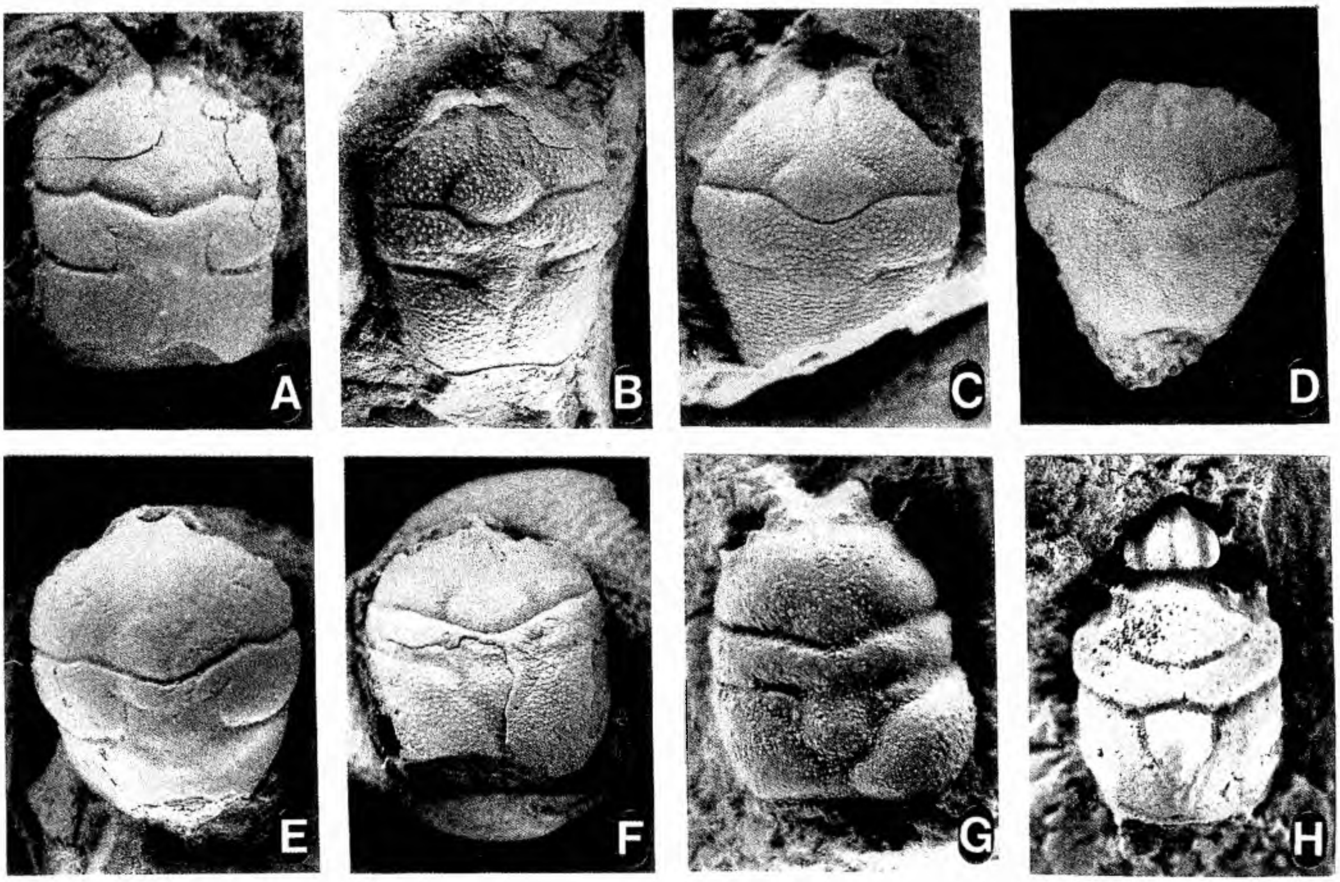

Fig. 18. Selected species of the family Prosopidae (subfamily Pithonotinae – **A-G**; subfamily Glaessneropsinae – **H**) (after Wehner, 1988); **A.** *Pithonoton aequilatum* (von Meyer), Malm β, Biburg at Weißenburg (Germany), BSP: 1980 XXX 480, carapace length (Cl) – 6 mm; **B.** *Pithonoton marginatum* (von Meyer), Tithonian, Štramberk (Czech Republic), Museum Brussel: Nr. 107; **C.** *Pithonoton serratum* (Beurlen), Malm δ, Geislingen at Steige (Germany), Museum Tübingen, Cl – 7 mm; **D.** *Pithonoton bidentatum* (Reuss), Tithonian, Murles at Montpellier (France), BSP: 1988 I 91, Cl – 11 mm; **E.** *Pithonoton grande* (von Meyer) (lectotype), Malm ε, Örlinger Tal at Ulm (Germany), BSP: 1881 IX 678, Cl – 14 mm; **F.** *Coelopus hoheneggeri* (Moericke) (holotype), Tithonian, Koniakau (Czech Republic), BSP: AS III 310, Cl – 7 mm; **G.** *Longodromites excisus* (von Meyer), isopod-infected specimen, Oxfordian, Spielberg at Hahnenkamm (Germany), BSP: 1988 I 90, Cl – 8 mm; **H.** *Glaessneropsis heraldica* (Moericke) (holotype), Tithonian, Koniakau (Czech Republic), BSP: AS III 306, Cl – 4 mm

praecursor Withers, based on well preserved specimens and Förster (1979b) described additional specimens. Both authors agree that this form is in many respects transitional between the macruran Glypheoidea and the early brachyurans, *i.e.* the Prosopidae (Fig. 20). This view became widely accepted suggesting that the origin of Dromioidea is quite clear, and is at least not in contradiction with palaeontological-morphological observations, in spite of some doubts (e.g., Števcić, 1971). *Eocarcinus* is transitional in many of its observable traits between the glypheoid, Middle Triassic *Pseudopemphix* and the prosopids, especially the earliest known species, *Eoprosopon klugi*, but a sudden reduction and displacement, as well as total disappearence of the postcervical furrow seems to mark a profound change during this stage of evolution (Fig. 20).

Similarity of early Galatheoidea to the earliest prosopids and to their probable ancestors (Förster, 1985b) suggests their common origin. Middle Jurassic *Gastrodorus* species, recently assigned to Galatheidae, is similar to *Eocarcinus* in its carapace form, well developed cardiac furrow, and in the shape of cervical and branchiocardiac furrows. Further Förster (1985b) suggests that *Gastrodorus* may be close to the ancestors of raninids, as it reveals similarities to the Cretaceous raninid genus *Notopocorystes*. Possibly it is not accidental that just these two probably constitute closely related groups (Brachyura and Galatheoidea) which were successful in brachyurisation.

The very close relationship of prosopids and the Homolodromiidae is universally accepted and seems to be well established by the high degree of similarity in carapace traits, patterns of furrows, ventral parts, and, partly, chelae as well. Wehner (1988) emphasized the close morphological similarity of *Foersteria* and *Homolodromia*, suggesting that the ancestors of homolodromiids might be close to *Foersteria*.

It is possible that cyclodorippoids may be derived in a similar way from prosopids, without a possibility for documenting this lineage in detail. Tavares (*pers. comm.*, 1995) has suggested that *Binkhorstia*, *Torynomma*, *Dioratiopus*, *Mithracites*, *Falconoplax* and *Eodorippe* should be excluded from the Cyclodorippoidea, and only some Tertiary *Cymonomus* and *Tymolus* fossil species should be regarded

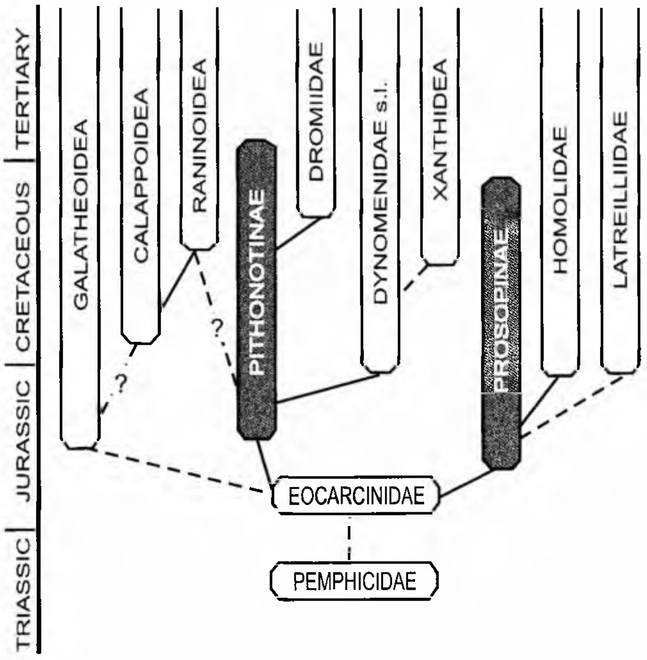

Fig. 19. Sketch of evolutionary relationships between prosopids, their presumed ancestor and descendants, based on their morphology

as belonging to that superfamily. These are both morphologically and temporally too distant from prosopids to recognise their exact relationship. The groove pattern and carapace form, apart from its flatness, of *Dioratiopus* much resembles that of some *Prosopon* and *Nodoprosopon* species (Wright & Collins, 1972). As *Dioratiopus* is excluded from this cyclodorippoids, this does not seem to offer a key for the origin of this superfamily.

Dromiids seem to be closely related to prosopids. Wright & Collins (1972) proposed that *Mesodromilites*, the earliest known crab (Albian) assigned to the Dromiidae, might be a descendant of *Rathbunopon*. In our view, *Rathbunopon* seems to be too specialised to be an ancestor of dromiids. Instead, there are a lot of traits common between the Pithonotinae and Dromiidae. *Pithonoton* and *Plagiophthalmus* in particular, seem to be close to dromiids, having an almost identical groove system, similar orbital grooves, and in some cases dromiid-like anterolateral spines as well. Further, young specimens of *Mesodromilites* have an elongated carapace in outline, quite close to *Plagiophthalmus* species. A similar, allometric growth is observed in Eocene *Dromilites* species (Wright & Collins, 1972). Hypothetically slight modification in carapace form (getting a circular outline, a shorter and spinose fronto-orbital margin) of a Pithonotinae species would result in a typical dromiid carapace.

Wehner (1988) proposed a prosopid origin of the Homolidae through *Laeviprosopon* and *Homolopsis* (cf. also Collins, 1997), following earlier authors cited by her. The carapaces of species belonging to these genera are extremely similar to *Prosopon* or *Longodromites*, but a clear presence of the *linea homolica* indicates their homolid status. Thus, this transition seems also quite probable, based on a wide variety of similar morphological traits. Wehner (1988) suggested also a prosopid origin for the Latreilliidae (see also Collins, 1997) based on a striking similarity of carapace outline, long rostrum, and strong, similar ornamentation of *Nodoprosopon ornatum* (von Meyer) and *Heeia villersensis* (Hée). Wright & Collins (1972) considered *Heeia* as belonging to the Latreilliidae.

The Dynomenidae as accepted by Glaessner (1969), include a set of genera (*Cyclothyreus* and *Palaeodromites*, Figs 21, 22, and *Dromiopsis*) probably closely related to the prosopids, more specifically to the Pithonotinae. As Wright & Collins (1972: 48) point out, "the shape of the carapace is indeed the only important character that divides Dynomenidae from Pithonotinae". The dynomenid position of the three genera mentioned, however, might be a matter of debate, despite their apparent by close relationships to that family.

Wright & Collins (1972) proposed a prosopid through dynomenid origin for the Xantidae, via *Palaeodromites* and *Xanthosia*. The carapace form and groove pattern of some *Palaeodromites* spp. seem indeed to be very close to those of *Xanthosia* forms. This last-mentioned genus was assigned by them in the Xanthidae. They proposed another, also dynomenid lineage leading to the Carpiliidae through *Diaulax*, *Caloxanthus* and *Paleocarpilius*. These proposed

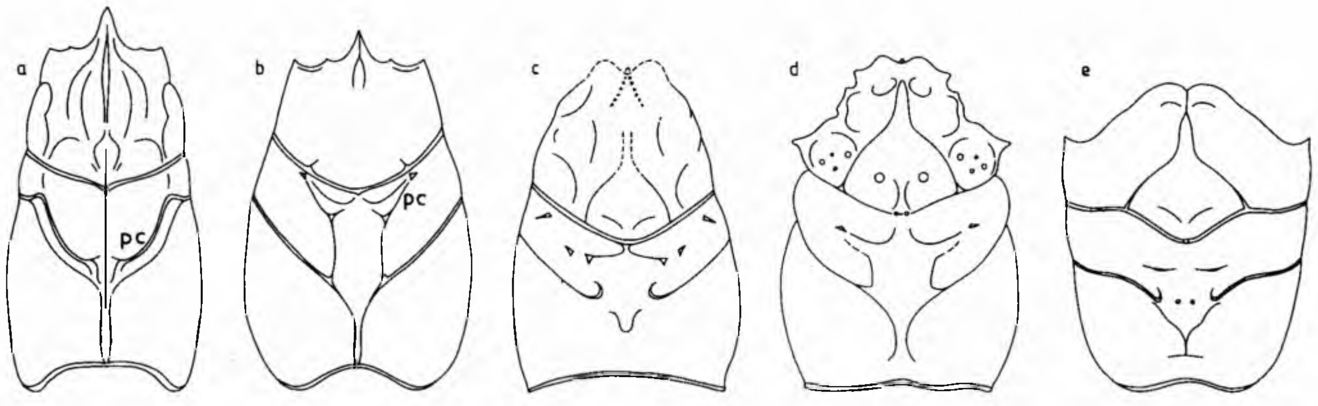

Fig. 20. Dorsal view of decapod carapaces , illustrating the presumed origin and early evolution of crabs (pc – postcervical groove, one of the most important line in phylogeny of decapods); a – *Pseudopemphix*, Middle Triassic; b – *Eocarcinus*, Lower Jurassic; c – *Eoprosopon*, Lower Jurassic; d – *Prosopon*, Upper Jurassic; e – *Pithonoton*, Upper Jurassic (after Förster, 1985a, 1986)

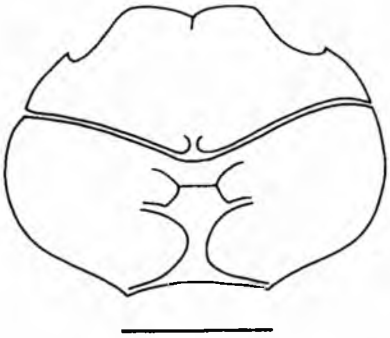

Fig. 21. *Cyclothyreus reussi* (Gemmellaro). Tithonian, Czech Republic (after Glaessner, 1969); dorsal view. Length of scale bar – 10 mm

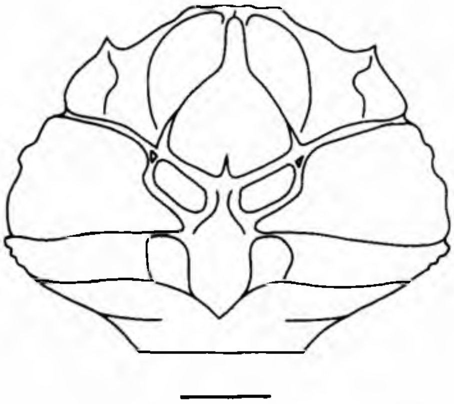

Fig. 22. *Palaeodromites incertus* (Bell). Cenomanian, England (after Glaessner, 1969); dorsal view. Length of scale bar – 5 mm

lineages are based on carapace morphology, apparently similar in subsequent members. However, these relationships seem to need additional validation.

Similarly, the origin of Calappoidea seems not to be well documented, although Förster (1968) (discussed by Wright & Collins, 1972) suggests a dynomenid (*Palaeodromites*) origin for *Paranecrocarcinus*, the earliest known calappoid. Furthermore palaeontological evidence strongly suggests a calappoid origin for raninoids.

ECOLOGY AND BIOGEOGRAPHY

by M. Krobicki (with G. Wehner's data)

Our knowledge of early, Jurassic crabs, is still rudimentary, based mainly on relatively few fossil occurrences. Despite the large number of modern crab species, about 4,500, we know little about their earliest progenitors. These results in part from their very low fossilisation potential (Schäfer, 1951), as discussed below, while a marked facies control is also a factor. This facies restriction is well demonstrated by European Jurassic prosopids. Examples discussed below are primarily based on Late Jurassic prosopids from Poland and Germany, whose geological setting allows reconstruction of their palaeoecology.

TAPHONOMY

The fossil record of decapods seems to be very poor when compared to that of most other shelled marine invertebrates. This is mainly due to their poor preservational potential. Carapaces and chelae of decapods have a proportionately large surface relative to their weight, meaning they are easily carried to the sediment surface until they are eventually destroyed. Consequently, these parts are embedded generally only in sediments deposited on low-energy conditions (Schäfer, 1951). Bioturbation often destroys the fragile tests (cf. Plotnick *et al.*, 1988) even after embedding. In this way, large tests (carapace width over about 5 cm) are positively sorted during taphonomic processes (Müller, 1993). As a result, decapods have a higher chance to be preserved on uneven bottoms containing low-energy traps ("pockets") in which the tests may be washed in, quickly buried, and preserved in internally poorly sorted and, as a rule, non-bioturbated sediments. Such conditions are widespread only on reefs and reef-like structures (Müller, 1993).

In the Oxfordian limestones of the southern Poland (vicinity of Kraków – see below), shrimps and lobsters occur together with prosopids (Krobicki, 1994a; Krobicki & Müller, 1998a, b). These three major decapod crustacean life-groups (the shrimps, lobsters, and crabs) differ basically in their fossilization potential. The first group is represented by actively swimming pelagic forms with a very thin cuticule or exoskeleton. Plotnick (1986), who studied taphonomy of modern shrimps, suggests that disturbances caused by scavengers and/or burrowing infauna are the major factor in destruction of buried arthropod remains. The time needed for decomposition and disintegration of shrimp bodies is less than nine days (Bishop, 1986b; Plotnick, 1986). The mode of life of shrimps and their thin cuticles make the probability of fossilisation very low. Therefore, the fossil record of natant decapods is extremely poor. More than 200 modern species are known, but only 30 fossil species (13.4%) have been described (Plotnick, 1986). Such a low chance of fossilization is limited to "exotic preservational environments" (Bishop, 1986b: 329).

From Plotnick's (1986) observations it may be concluded that the fossilisation potential of crabs and lobsters is much higher than that of shrimps (see also Bishop, 1986b). Thus, the presence of shrimps in the small sponge bioherms of massive limestones in the vicinity of Kraków (Dolina Szklarki valley) indicates a relatively high probability of fossilisation of decapods in this environment. The cuticle of decapods is composed of chitin and protein, which is frequently calcified (Richards, 1951). Decomposition of the chitin by fungi, bacteria, actinomycetes, nematodes and protozoa (Plotnick, 1986) hinders preservation of arthropod remains. Basan & Frey (1977) suggest that the major factor in the destruction of these remains is the dissolution of calcite in the exoskeleton (Speyer, 1991; Plotnick *et al.*, 1988). In comparison with the so-called fossorial "shrimps" (*Callianassa*, *Ctenocheles*, *Thalassina*, and *Upogebia*), the true shrimps have a lower fossilization potential, while crabs and lobsters have a better one.

Along with biological decomposition of carapaces, the Mesozoic prosopid tests suffered from physical disturbance,

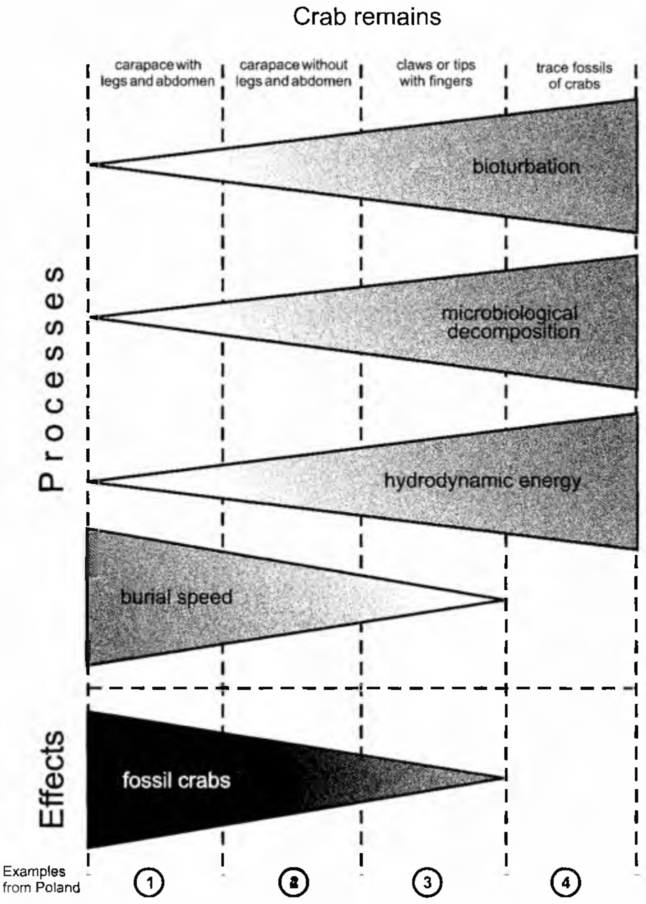

Fig. 23. Taphonomic conditions of crab remains in relation to rate of sedimentation, physical and biological processes. Examples from Poland: *1* – Flysch Carpathians (Oligocene), Jerzmańska (1967); *2* – Oxfordian and Tithonian crabs (this paper); *3* – Fore-Carpathian Depression (Miocene), Förster (1979a); *4* – Fore-Carpathian Depression (Miocene), Radwański (1970)

destructive transport, chemical breakdown, and bioturbation. The only way to avoid disintegration under these conditions is fast burial of carapaces or their preservation in burrows. Burrowing is widespread among lobsters (e.g., within the modern genera *Nephrops* and *Homarus* and Cretaceous *Linuparus*; see Pemberton *et al.*, 1984), shrimps (mainly *Callianassa*, *Upogebia* and *Thalassina*, which are responsible for many crustacean-type ichnofossils; cf. Frey & Howard, 1969; Frey *et al.*, 1978; Förster & Barthel, 1978) and numerous crabs (mainly species of the genera *Uca*, *Ocypode*, *Sesarma*, *Macrophthalmus* and others; cf. Frey *et al.*, 1984; Dworschak & Rodrigues, 1997). On the other hand, the decapod remains preserved within their burrows are very rare: several species of the lobster genus *Glyphaea* (e.g., Sellwood, 1971; Bromley & Assgard, 1972), shrimps of the genus *Callichirus*? (Stilwell *et al.*, 1997), *Cambarus*? (Hasiotis & Mitchel, 1989), modern species *Axianassa australis* Rodrigues & Shimizu (Dworschak & Rodrigues, 1997), and crabs (e.g., *Longusorbis*, *Antarctidromia*) (Richards, 1975; Förster *et al.*, 1987). However, up till now no direct evidence for burrowing has been found among the Jurassic prosopids. Possibly, the only chance for the preservation of crab fragments was fast burial of their carapaces after death or moult, particularly in sediments which were subsequently not bioturbated or redeposited (cf. Plotnick *et al.*, 1988 for concise review of moult cycle = ecdysis, and their significance in the fossil record). Such sediments were frequently deposited within sponge bioherms. Additionally, the massive structure of these buildups might protect the remains from scavengers.

Warner (1977) distinguished four modes of life of modern crabs: (1) walking, running, and climbing, (2) swimming, (3) burrowing, and those (4) incorporating camouflage. Prosopids probably belonged to the first or fourth group. The analysis of the Upper Jurassic material from southern Poland suggests that post-mortem preburial interactions between organisms and the environment (Krobicki & Müller, 1998a, b) were important factors in the formation of a fossil thanatocenosis (cf., Lawrence, 1968). This may be concluded from the observations of a totally accidental occurrences of crab remains in cyanobacterial-sponge bioherms and/or biostromes.

The hydrodynamic energy of the environment caused disintegration of individual fragments. After comparing the Oxfordian and Tithonian fossils from Poland with other, mainly Tertiary examples from Poland, a schematic model is proposed to explain the relationships between taphonomic processes and biological-sedimentological factors. Four categories of decapod remains have been distinguished (Fig. 23): 1 – carapace with legs and abdomen; 2 – carapace without legs and abdomen; 3 – claws or tips of fingers; 4 – trace fossils of crabs. Considering all possible means of destruction, it seems that the intensity of bioturbation and microbiological decay are of the most crucial biostratinomical factors. Their higher intensity decreases the chances for preservation of crab fossils (e.g., Plotnick *et al.*, 1988; Heikoop *et al.*, 1997). The carapaces may be completely eliminated from a thanatocenosis and, eventually, even the most resistant elements as chelae or finger tips may be absent (Speyer, 1991).

In the described case from the vicinity of Kraków, intensive burrowing and bioturbation are common within platy limestones (e.g., ichnogenus *Thalassinoides*). Glypheoids might have created some or even most of these burrows, despite the absence of their fossils within them. The structures prove that the deeper parts of the sediment were colonized by burrowing animals. The intensive bioturbation of the top layer led to its homogenisation. The lack of an initial lamination also results from bioturbation (Bromley, 1990; Hoffmann & Uchman, 1992).

When hydrodynamic energy increased, even living decapods could be crushed into pieces and, therefore, the Jurassic prosopids tended to take refuge within biogenic carbonate buildups, which were largely resistant against mechanical destruction. Contrary to the processes mentioned, any increase in the sedimentation rate was protective, resulting in a positive taphonomic feedback (Fig. 23) (cf. Bishop, 1987).

Rarely, fossil crab-rich deposits may be found. For instance, the so-called *Dakoticancer* assemblage (the Upper Cretaceous Pierre Shale, South Dakota) reveals an astonishing abundance. Bishop (1981) collected five thousand decapods from this formation. Such decapod-rich assemblages seldom appear in the fossil record. Another example is the formation of carbonate or phosphate concretions around dead individuals, protecting tests effectively from further disintegration. Such concretions positively facilitate recognition and collecting of fossil decapods (cf. Speyer, 1991; Feldmann *et al.*, 1993; Heikoop *et al.*, 1997). Due to such preservation there are known decapod-rich assemblages from various sedimentary environments (Cretaceous examples are given by Bishop, 1981, 1986b; Tertiary by Mundlos, 1975; Förster *et al*,. 1987). In extreme cases, exceptional preservation may took place, e.g., complete specimens of syncarid (*Palaeocaris typus* Meek & Worthen) or paleocarid (*Belotelson magister* Packard) shrimps, cycloid maxillopodan crustaceans (*Cyclus*, *Halicyne*, *Apionicon*) or phyllocarid crustaceans of genus *Kellibrooksia* from the Middle Pennsylvanian of NE Illinois (Mazon Creek) (Baird *et al.*, 1985, 1986; Baird, 1997; Schram *et al.*, 1997) and genus *Dithyrocaris* from the uppermost Westphalian of England (Anderson *et al.*, 1999), suggesting very rapid burial and an immediate formation of concretions. Sporadically decapod remains are also found within cephalopods and other organisms (as scavengers), but these events need extremaly rapid burial processes (cf. Tshudy *et al.*, 1989; Fraaye & Jäger, 1995).

Jurassic prosopids have never been found within concretions. Consequently, they have been preserved as detached carapaces or limb parts, frequently as casts only. This is the reason for a relatively poor fossil record of the Jurassic prosopids, while, furthermore, some of the species are known from one or few specimens only. This, of course, hinders palaeobiological studies and reconstruction of phylogenetic relationships, precluding possibilities of recognition of variability within species, ontogenesis, aut- or synecology, etc. (Förster, 1985a, 1986). Their generally poor preservation also restricts palaeoecological study.

ECOLOGY AND STRATIGRAPHIC DISTRIBUTION OF PROSOPIDS

Comparison of modern and Late Jurassic environments, leads to the conclusion that living and sheltering within reefs or reef-like structures was an effective defense mechanism against destructive physical and biological factors. Currently, such phenomena are known to occur on a large scale. For instance the widespread Indo-west Pacific genus *Trapezia* massively lives within colonies of *Pocillopora* corals (e.g., Warner, 1977). Another type of commensalism is that of hepalocarcinid crabs with pocciloporid corals. Prahl (1983) illustrated members of the Hepalocarcinidae family (e.g., *Hepalocarcinus marsupialis* Stimpson, *Pseudocryptochirus crescentus* (Edmonson)) living in caverns of galls in coral colonies, where the females pass their entire lives. Bishop (1986b) mentioned shallow-water polychaete reefs, where 29 species of decapods were found; out of them 25 lived exclusively within reefs (see also Bertini *et al.*, 1998; Sousa Dias & Paula, 1998). Oyster crabs (*Panopeus herbstii* Milne-Edwards) permanently dwell within oyster banks off the coast of Gulf of Mexico (Wells, 1961). They coexist with blue crabs (*Callinectes sapidus* Rathbun) which may even effectively limit the oyster distribution, particularly that of young specimens. In turn *Eurypanopeus depressus* (Smith) is a scavenger, usually hiding under sponges and in oyster clusters, but *Pinnotheres ostreum* Say lives as a commensal (or parasite) in the mantle cavities of oysters (Wells, 1961). Within the Danian mussels commonly occur *Pinnotheres* sp. remains. Some crabs utilise other organisms for camouflage; e.g., Dromiidae, as the sponge crab *Cryptodromia hilgendorfi* de Mann (probably a distant descendant of Jurassic prosopids), living off the Australian coast, is such a spectacular example, using sponges and compound ascidians both as places to live in and for concealment (McLay, 1982, 1983). This species exploits mainly sponges, especially of genus *Suberites*, in a commensal relationship. However, the pinnotherid crabs *Pinnotheres laquei* Sakai live within the mantle cavity of the terebratulid brachiopods *Laqueus rubellus* (Sowerby), without visible deformations both valves and lophophore loop, and represent the commensal too (Feldmann *et al.*, 1996).

Tertiary strata of the Paratethys include numerous examples of biogenic buildups (reefs, bioherms, biostromes, and banks) were inhabited or utilised by decapod crustaceans. Müller & Collins (1991) described a rich Late Eocene fauna associated with corals from Hungary, including *Tetralia* species: the extant representatives of which genus are obligate commensals with corals. A case similar to that of extant *Trapezia* species was suggested for the Middle Miocene Paratethyan *Trapezia glaessneri* Müller, associated with seriatoporid coral *Stylophora subreticulata* Reuss within the same reef bodies (Müller, 1984). It is known that *Trapezia* species are commensal with seriatoporid corals (Garth, 1974). Yanakevich (1969) described crabs (among others *Daira*) from the Miocene (Badenian) bioherm limestones of NW Moldavia, which occur together with rich bivalve fauna. Neogene *Daira* in Europe and in the Indo-west Pacific seems to be restricted to reef structures. Numerous fragments of crabs (mainly chelae) were found in the Polish part of the Carpathian Foredeep by Förster (1979a), some of which came from bryozoan-red algal reefs and small coral patch reefs (*Tarbellastrea reussiana* Milne-Edwards & Haime). In Late Pleistocene of Oregon, pinnotherid crabs *Pinnixa faba* (Dana) occur within the pelecypods *Tresus capax* (Gould) (Zullo & Chivers, 1969).

Most prosopid species were found in Upper Jurassic limestones, deposited on deep sublittoral to littoral settings, abundantly containing sponges, and sporadically hermatypic corals as well. A part of these limestones were formed on muddy to sandy bottoms, but most were formed in bioherms or true reefs. This environment included a multitude of habitats, which was characterised by a high degree of substrate complexity, offering shelter, but almost universally retaining some internal patches with soft sediment for burrowing animals. Although it is difficult to reconstruct the ecology of individual prosopid species, their high diversity of form and abundance may well be connected to this manifold environment. The brachyuran body might have helped adaptation to these environments in many ways. Possibly, the more compact body of crabs, if compared to lobsters and shrimps, enabled easier modes of locomotion, concealment, or other means of self-protection, and thus offered fewer possibilities for attack by predators when compared to macruran decapods. On the other hand, some are quite spiny. The great success of the brachyurans is evident from the enormous taxonomic and morphological diversity of early and late crabs (Förster, 1985a).

Some early species, including the earliest prosopid, *Eoprosopon klugi* and the Cretaceous *Ekalakia lamberti* lived on soft, siliciclastic substrates, indicating that early crabs were by no means restricted to bottom with carbonate sediments, or to bioherms. Cretaceous forms occur only exceptionally in reefal facies (Via Boada, 1981).

Middle Jurassic

All species of Middle Jurassic Prosopidae described so far come from shallow or moderately deep marine environments. The oldest prosopid species, *Eoprosopon klugi* from the Upper Pliensbachian of Franconia, probably lived in the same habitat (on a silty sea floor) as did the first known crab, *Eocarcinus praecursor* from the late Early Pliensbachian. The mode of life of prosopids could be similar to that of their presumed ancestors (Pemphicidae) who were probably also shallow water carnivores, herbivorous, or scavenging organisms. Considering the poor geological record of Middle Jurassic prosopids, it is difficult to make any deductions about their palaeoecology. However, most seem have lived in shallow, warm waters within organic buildups such as coral limestones in France (*Foersteria auduini* (Deslongchamps), *Coelopus bigoti* Hée, *C. moutieri* (Hée), *Nodoprosopon langrunensis* (Hée)) and Tanzania (*Foersteria lugobaensis* (Förster)), or brachiopod shell beds in Germany and Austria (*Nodoprosopon*? *vilsense* (Stolley)) (Förster, 1985b).

Upper Jurassic

The very strong and sudden development of prosopids took place during the Late Jurassic, probably due to the vast expansion of sponge, sponge-coral, or coral biohermal and reef structures in Europe, and possibly, elsewhere on the margins of the Tethys Ocean (Krobicki & Müller, 1998a, b, c). A wide variety of different environments were offered here, enabling the survival of the small crabs and promoting their evolution. The family flourished during this time as it is reflected by the high number of species and specimens.

Examples of Oxfordian, Kimmeridgian, and Tithonian environments where prosopids lived are presented below. Reconstructions were based on investigations of two authors (G. W. and M. K.), and supported by the analyses of numerous literature data.

Oxfordian

The Oxfordian sponge megafacies is widely spread in Europe from Portugal to Romania. It was formed in a deep-neritic environment, parallel to the northern margin of the Tethys. The first numerous Oxfordian prosopids occur in small sponge bioherms of Middle Oxfordian (Poland) and Upper Oxfordian (Germany) age; in both cases the buildups are isolated bodies within platy limestones.

Poland. Oxfordian strata are developed in three facies in the southern part of the Polish Jura, around Kraków (Figs 24–26). They begin with (i) well-bedded micritic, platy limestones which were initially deposited in the Middle Oxfordian, and contain numerous ammonites, rare benthic fauna (brachiopods, bivalves), and of decapods (glypheoid lobsters). Subsequently, the massive limestones (ii), primarily representing small sponge bioherms (*ca.* 2 m high and 3–4 m wide), were developed within these limestones. The first crabs in this area, *Pithonoton serratum* (von Meyer), *P. insigne* (von Meyer), *Nodoprosopon heydeni* (von Meyer), and rare shrimps (*Aeger* sp.) have been found only in these small, loose sponge bioherms, while isolated lobsters (*Glyphea* sp.) exclusively occur within platy limestones surrounding the bioherms (Dolina Szklarki valley; Figs 24–26; Krobicki, 1994a; Krobicki & Müller, 1998a, b). Similar relations were recognised in other areas of the Polish Jura and in the south-western Mesozoic margin of the Holy Cross Mountains (central Poland). At these locations numerous crab fauna (mainly prosopids) has been described from the Middle and Upper Oxfordian (Barczyk, 1961; Collins & Wierzbowski, 1985). Separate findings of glypheoid lobsters, *Glyphea* (*Glyphea*) *muensteri* (Voltz) in Central Poland Uplands are connected with occurrence of the platy limestones (Förster & Matyja, 1986).

In the Upper Oxfordian (Bimammatum or Planula Chron of the Kraków Upland), the massive facies (ii) dominates significantly and interfingers with the next facies (iii) of well-bedded limestones with abundant cherts. Within the massive (ii) and bedded-type (iii) limestones there are numerous siliceous sponges (up to 50 % by volume of a rock) and such as benthic animals: brachiopods (terebratulids – 62%, rhynchonellids – 10%), crabs (8%), and bryozoans, serpulids, bivalves, crinoids (the last four make 4%), and also cephalopods (ammonites – 10%, belemnites – 6%), as well as widespread stromatolite crusts (cyanobacteria and blue-green algae). Siliceous sponges formed the cyanobacteria-sponge bioherm structures which are characterised by a rigid framework during bioherm growth (Matyszkiewicz, 1994, 1997). Numerous crabs were often found in the cavities of the framework structures, being accompanied by brachiopods (*Terebratulina substriata* (Schlotheim)) and serpulids. Crabs are the most abundant in the last mentioned two facies. Even though they constitute a small percentage of the total faunal assemblages (max. 8% = 125 specimens – at Kraków-Zakrzówek; Figs 24–26); this is an extremely high number for fossil decapods. In this locality crabs are accompanied by numerous brachiopods, mainly from the Dallinidae family (*Dictyothyropsis loricata* (Schlotheim), *Cheirothyris fleuriausa* (d'Orbigny), *Ismenia recta* (Quenstedt)) and Thecideidae, characteristic for reef structures. The representatives of Prosopidae dominate there (96.8%), including: *Pithonoton serratum* (68.8%), *P. insigne* (13.6%), *Pithonoton* sp. (11.2%) and *Nodoprosopon heydeni* (3.2%). The list is completed by *Laeviprosopon laeve* (von Meyer) (Homolidae; 3.2% of the total crab remains). Relative proportions at family level are nearly identical between the Kraków area and the Wieluń Upland (Collins & Wierzbowski, 1985) (Fig. 28).

Germany. Small algal-cyanobacteria-sponge bioherms, about 4 m high by 3 m wide, occur within well-bedded limestones in Upper Oxfordian (Planula Chron) of the Franconian Alb (Germany; vicinity of Biburg, Fig. 27). Some 50 percent of these structures are built of stromatolites and al-

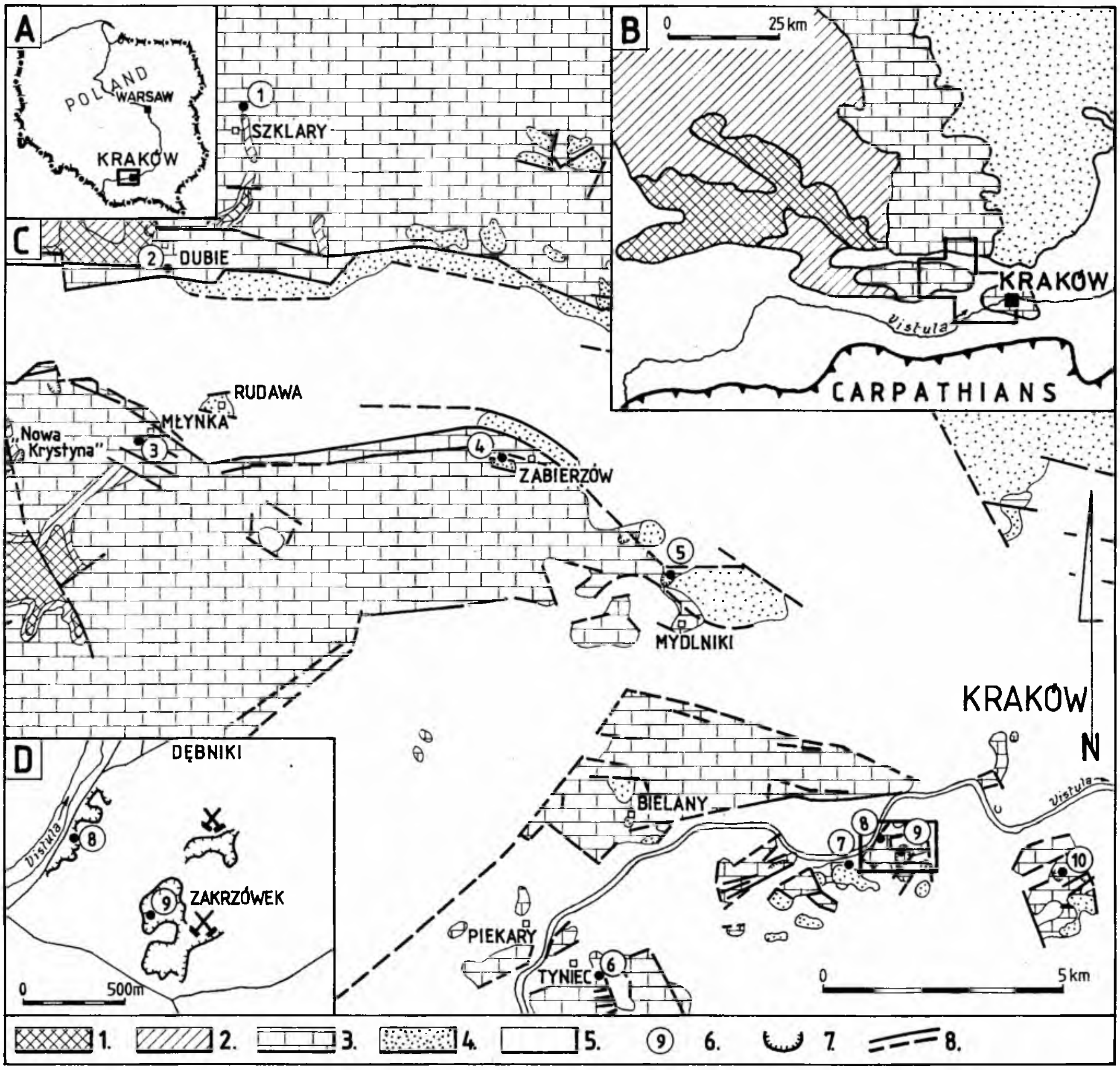

Fig. 24. Location of the Oxfordian outcrops with crabs within southern part of Polish Jura. Geological map after Gradziński (1972, simplified) (C); *1* – pre-Jurassic deposits; *2* – Middle Jurassic; *3* – Upper Jurassic; *4* – Cretaceous; *5* – Tertiary; *6* – locations with decapod fauna; *7* – quarry; *8* – faults

gal crusts with numerous (up to 25%) sponges (*Stauroderma*, *Thyroidium*, hexactinellid species). The macrofauna of these bioherms is abundant and includes mainly brachiopods (50%), ammonites (25%), and bivalves (15%), while the microfauna is represented mainly by numerous foraminifers (Scheirer & Yamani, 1982). Decapods compose up to 10 percent of the fossil assemblages (over 7,000 species). Prosopid crabs prevail (92.4%) within this group, and are represented by: *Pithonoton serratum* (Fig. 18 C) (57% of the total), *P. aequilatum* (von Meyer) (Fig. 18 A) (6%), *P. insigne* (Fig. 17 K, L) (0.8%), *P. grande* (Fig. 18 E) (0.4%), *Nodoprosopon spinosum* (von Meyer) (Fig. 17 F) (26%), *N. torosum* (von Meyer) (Fig. 17 H) (0.7%), *N. bucculentum* Wehner (0.4%), *N. ornatum* (0.3%), *Foersteria biburgensis* (Fig. 17 D) (0.5%), *F. cornuta* Wehner (0.3%). The remaining decapods represent the Homolidae (*Gastrodorus neuhausense* von Meyer; 6%), Erymidae (*Eryma* sp.; 0.4%), Mecochiridae (*Mecochirus* sp.; 0.4%), and Axiidae (*Magila* sp.; 0.8%) (Wehner, 1988).

This abundance of the crab fauna (both in Poland and Germany) must have been initially even bigger, considering information losses estimated by Lawrence (1968) at 25 percent (only this portion of a living community is currently present as a fossil assemblage). This would suggest that the initial abundance of crab communities was about four times higher than the number of fossils species observed today, which might be a very rough estimate. Considering that several moult stages of one particular individual may be preserved in a fossil assemblage, the abundance of a living population cannot be estimated from a simple recalculation

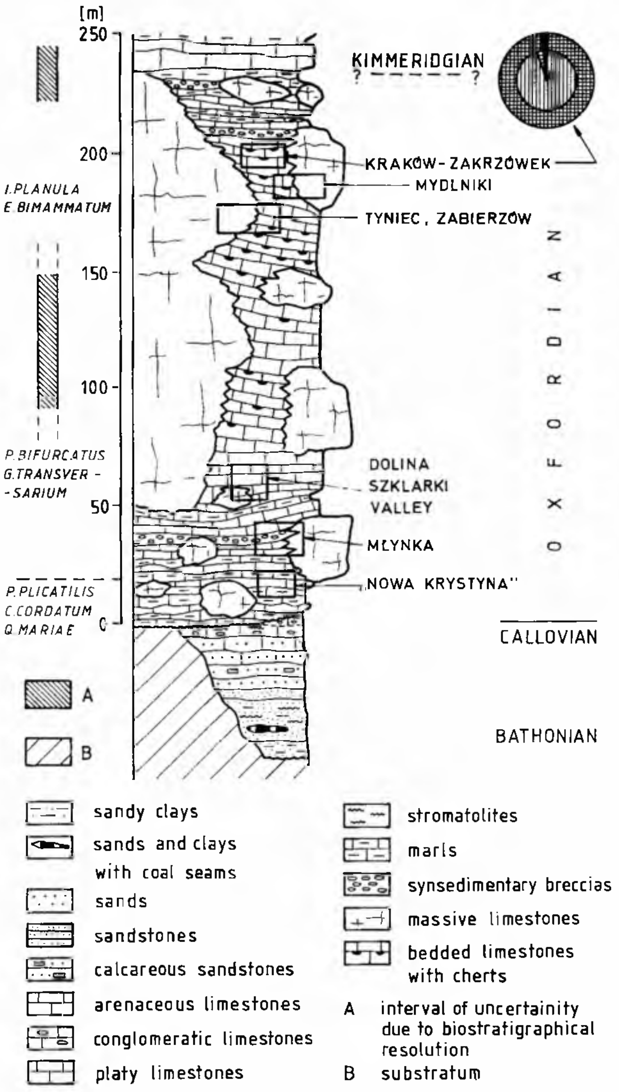

Fig. 25. Geological sequence of the Jurassic strata in the vicinity of Kraków (after Matyszkiewicz, 1994). Rectangles indicate the approximate positions of locations with crab fauna – see Figs 24, 26. Crab pie chart – see Fig. 28

of Lawrence's correction factor. Nevertheless, never earlier and never later in their Jurassic–Cretaceous history did prosopids occur so abundantly and over such a vast area (Fig. 28).

The depth of deposition of the Oxfordian sediments has been a permanent source of debates. The facies of cyanobacteria-sponge bioherms was initially regarded as the sediment of a deeper part of the shelf (Dżułyński, 1952). A contrasting opinion was presented for identical sponge bioherms of the Swabian Alb (Schorr & Koch, 1985; Wirsing & Koch, 1986), from where most Oxfordian prosopids had been described for the first time ever (Meyer, 1860). The lack of the fauna diagnostic for bathymetry additionally hindered the unequivocal determinations of depth during sedimentation of these buildups. The latest stratigraphical and sedimentological investigations lead to the conclusion that these carbonate buildups occurred at depth about a few hundred metres, but the paleorelief between the tops of huge cyanobacteria-sponge complexes of the Central Polish Upland and the surrounding them well-bedded limestones could exceed 200 metres, particularly in the Late Oxfordian (Matyja & Wierzbowski, 1996). However, Pisera (1997) suggested deeper sedimentary environment, reached even about 900 metres on the Late Jurassic Swabian Alb shelf, as a part of northernmost Tethyan margin, but this opinion was based on erroneously supposition of existance of 1° slope inclination of this shelf (but modern shelf analogues indicate only 0.1° inclinations – e.g., Schopf, 1980). Additionally, Matyszkiewicz (1997, 1999) discussed bathymetry and the primary sea-bottom relief of these Oxfordian biostructures, and suggested both shallower (neritic) depositional environments and smaller relief attaining maximum about 100 metres than authors mentioned previously. On the other hand, as suggested Leinfelder (1993), pure siliceous sponge reefs possibly did not occur deeper than 120 metres. Such a statement would automatically set the bathymetric limits for the Oxfordian prosopid crabs, which could probably live either within the rigid framework of sponge buildups, or also in the inter- or peri-bioherm environments surrounding these structures (Merta, 1972; Nitzopoulos, 1973; Figs 23, 27). If this model of sedimentation is accepted for the Oxfordian sponge-megafacies of the Germany (Swabian-Franconian Alb), France, Spain, and Portugal (for references see Leinfelder, 1993; Leinfelder *et al.*, 1994), the local prosopids would prefer similar environmental conditions.

When we compare with sponge facies, Oxfordian coral reefs were rare on the carbonate platform of the European

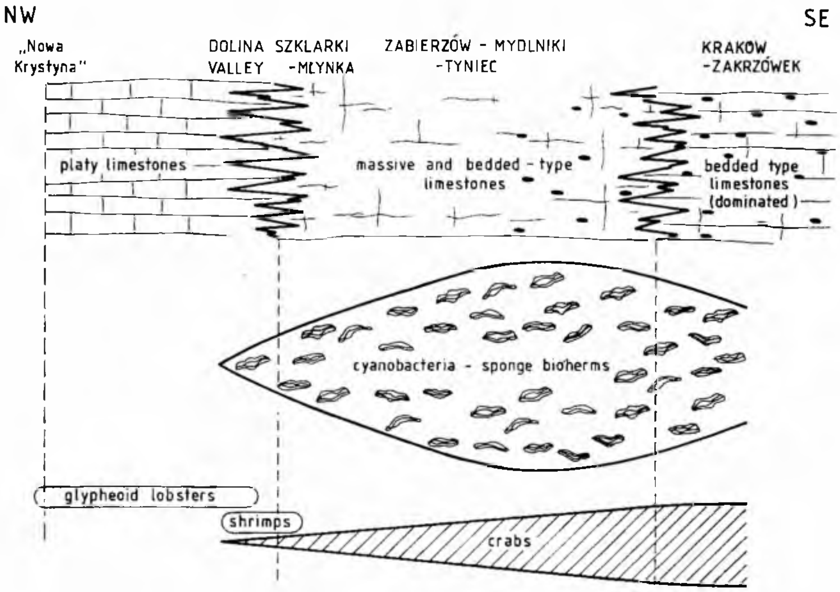

Fig. 26. Schematic sketch of distribution of decapod crustaceans fauna in respect to main Oxfordian facies in environs of Kraków, soutern Poland. Note the diachronous facies relations between carbonate deposits

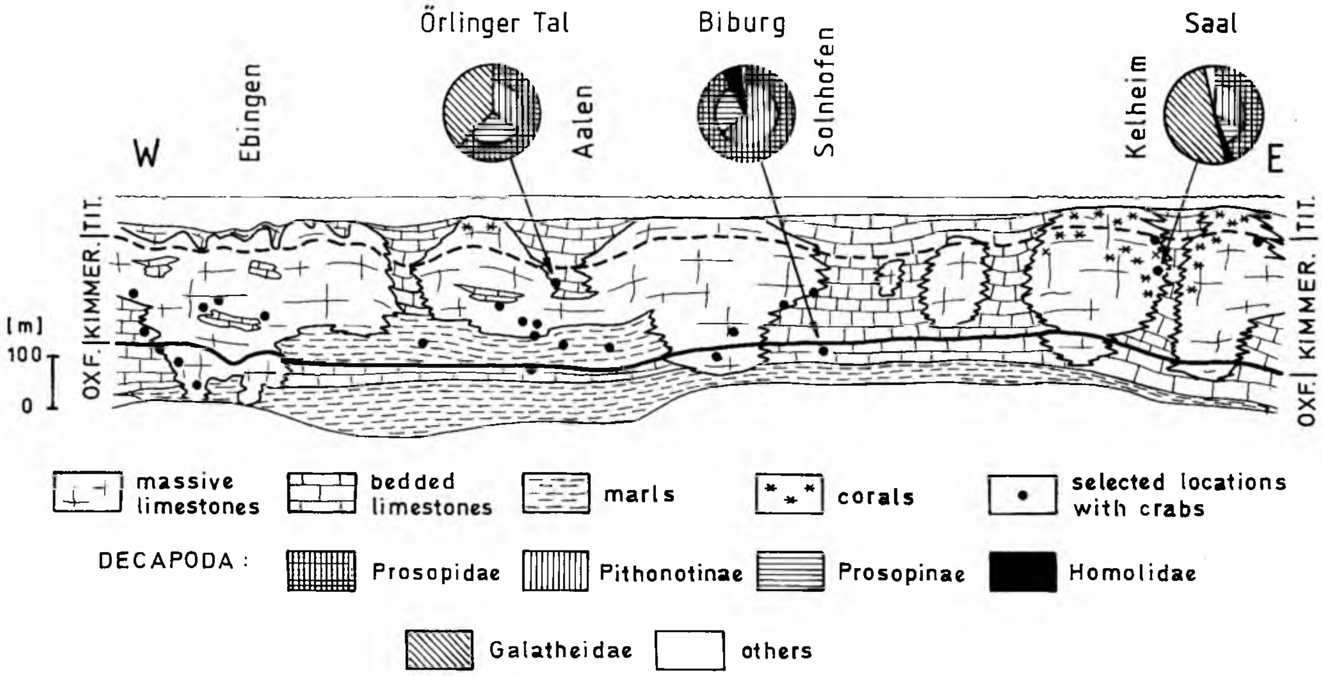

Fig. 27. Distribution of decapod crustaceans in Oxfordian and Kimmeridgian strata of Franconian-Swabian Alb (southern Germany). Geology after Meyer & Schmidt-Kaler (1989, generalized). Note the connection between pie chart compositions and facial/age positions

Tethyan shelf, characterised mainly by the occurrence of small coral patch reefs. Oxfordian coral assemblage in the Stránská Skála Hill, near Brno (Czech Republic) (Eliáš & Eliášová, 1984) is dominated by *Isastraea helianthoides* (Goldfuss) and *Thecosmilia trichotoma* (Goldfuss) (Eliášová, 1994). Oppenheimer (1926) listed the fauna record of this locality, including 90 species, two of which were prosopids: *Prosopon aculeatum* von Meyer and *Pithonoton rostratum* von Meyer (see also Jaroš & Zapletal, 1928). Bertling & Insalaco (1998) described Middle Oxfordian coral/microbial reefs from the northern Paris Basin, and mentioned very rare crustacean fauna (*Pithonoton* sp.) which were found in reef rubble facies dominating by coral branches of *Dendrohelia coalescens* (Goldfuss). The depositional environment of this facies very well corresponds to the back-reef of shallow (no more than a few metres) upper subtidal zone (Bertling & Insalaco, 1998).

A poor diversity of this crab fauna, probably the result of collecting biases, is however very interesting from a palaeoecological point of view. This indicates that as early as the Oxfordian, the prosopid fauna inhabited in the coral reef environment as well.

The high correlation of decapod associations with reef building organisms suggests the existence of a specific ecologic interrelationship between reef organisms and these decapods. This is partly due to the symbiotic relationship between these organisms. Small prosopids and shrimps might have used the small sponge bioherms as hiding places from potential predators, especially during a soft-shelled moulting stages. Additionally, a bioherm might help them survive because of its massive and rigid framework structures, in contrast to unfavourable soft carbonate muds surrounding the bioherms. Thus, the close relationship between crabs, shrimps and the locally abundant sponge bioherms was probably (without direct evidence) commensal in its character (0+, *sensu* Ager, 1963), *i.e.* a close symbiotic relationship where one species benefits (+ = crabs) and the other remains unharmed (0 = sponges).

On the contrary, big lobsters, having large appendages and stronger carapaces, could better move on a soft carbonate mud bottom among bioherms. They probably produced the *Thalassinoides* burrows in the soft sea-floor.

Kimmeridgian

Prosopids are known almost exclusively in the Franconian-Swabian Alb (Germany) within massive, sponge-dominated limestones in the Kimmeridgian of Europe. The sponge buildups reach a height of 100 m. Initially, small, then larger coral and coral-hydrozoan reefs appear within them (Meyer, 1975; Meyer & Schmidt-Kaler, 1989) (Fig. 27). The coral-hydrozoan reefs are built mainly of corals of the genera: *Thecosmilia*, *Dermosmilia*, *Ovalastrea* and *Calamophylliopsis*, often with algal crusts. Small crabs may sometimes be found within the centers of massive *Thecosmilia* corals because the small Jurassic prosopids could probably find a refuge (Wehner, 1988) in the labyrinth-like structures of these colonies. The most abundant assemblages of the Kimmeridgian decapods are known from two locations: Saal near Kelheim (Franconian Alb) and Örlinger Tal near Ulm (Swabian Alb). In both these sites, approximately half of the assemblage is composed of the galatheid *Gastrosacus wetzleri* (Saal: 49% of the total, Örlinger Tal: 33%) (Figs 27, 28). The remaining portion of both assemblages is made up almost exclusively of prosopid crabs, among which *Longodromites excisus* is predominant (21% and 14%, respectively), accompanied by species of *Pithonoton* (8% and 15%), *Prosopon* (6% and 4%), *Nodoprosopon* (3.7% and 22%), *Lecythocaris* (0.7% and 0.5%), and

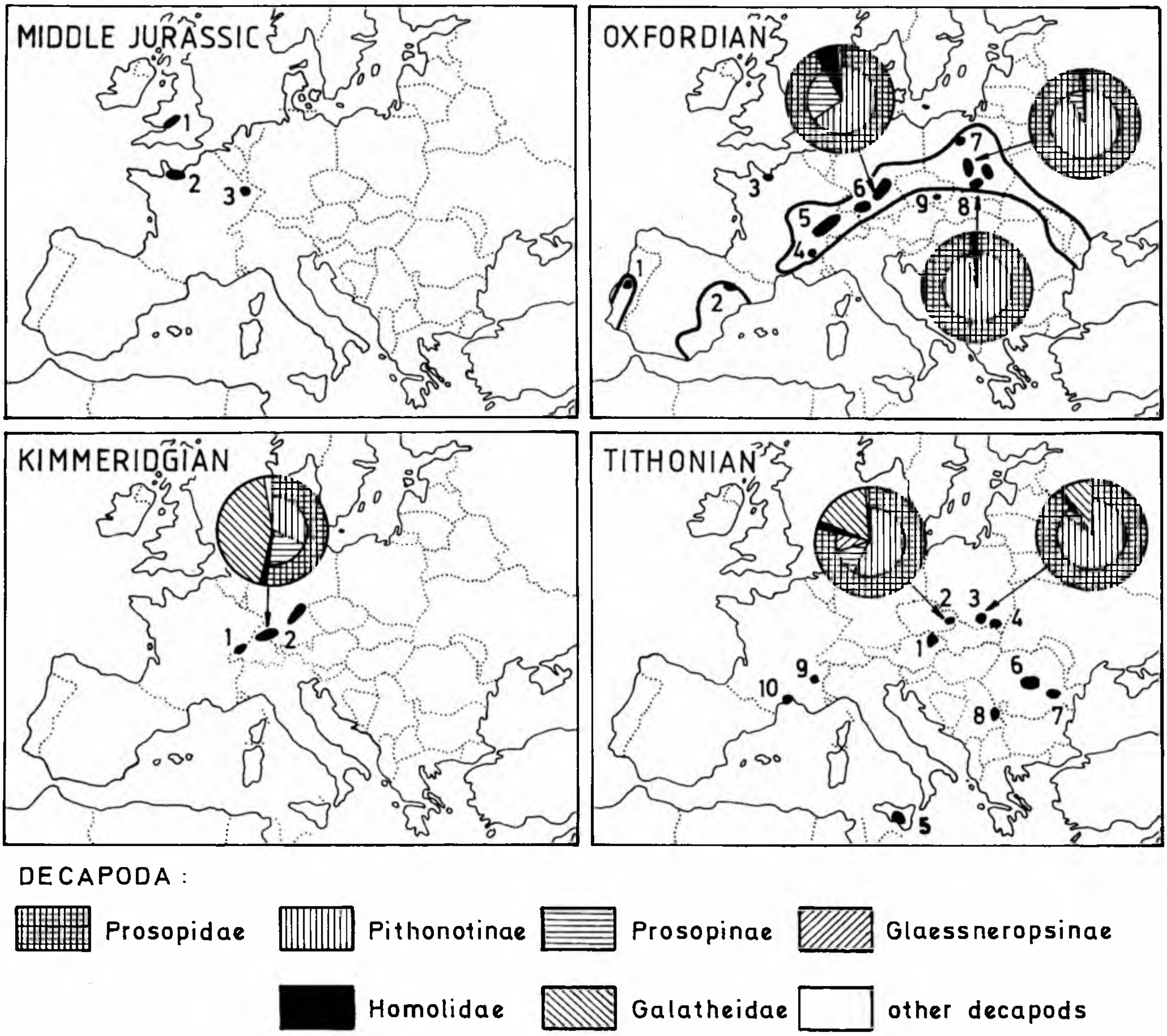

Fig. 28. Distribution of Prosopidae from the Middle Jurassic to Tithonian time in Europe. Solid line in the Oxfordian map indicates the probable extent of the sponge megafacies in Europe (after Matyja & Wierzbowski, 1995, simplified); black dots on the Tithonian map indicate places with the Štramberk facies in the Carpathians, Moesian Platform and surrounding areas. Explanation of numbers: **Middle Jurassic**: *1* – England (Somerset, Wiltshire, Oxfordshire); Morris, 1980. *2* – France (Calvados); Hée, 1924. *3* – France (Dept. Mosel); Glaessner, 1933. **Oxfordian**: *1* – Portugal (Cabaço); Wehner, 1988. *2* – Spain (Moneva/Zaragoza); Via & Sequeiros, 1993. *3* – France (Dept. Jura); Van Straelen, 1925. *4* – France (Dept. Isère); Wehner, 1988. *5* – France & Switzerland; Wehner, 1988. *6* – Germany (Franconian-Swabian Alb); von Meyer, 1860; Wehner, 1988. *7* – Poland (Kujawy region, Holy Cross Mts., Polish Jura); Collins & Wierzbowski, 1985. *8* – Poland (Kraków region); Krobicki, 1994a and this paper. *9* – Czech Republic (Stránska Skála Hill); Jaroš & Zapletal, 1928. **Kimmeridgian**: *1* – Switzerland (Kanton Bern); Thrumann & Etallon, 1861. *2* – Germany (Franconian-Swabian Alb); von Meyer, 1860; Wehner, 1988. **Tithonian**: *1-8* – Štramberk limestone facies: *1* – Austria (Ernstbrunn); Bachmayer, 1955. *2* – Czech Republic (Štramberk); Moericke, 1889; Blaschke, 1911. *3, 4* – Polish Carpathians: *3* – Woźniki (Patrulius, 1966); *4* – Kruhel Wielki; Wójcik, 1914. *5* – Italy (Sicily); Gemmellaro, 1869. *6* – Romania (Carpathians); Lorenthey & Beurlen, 1929; Patrulius, 1966. *7* – Romania (Moesian Platform); Muţiu & Bădăluţă, 1970, 1972. *8* – Serbia; Wehner, 1988. *9* – France (Grenoble); Wehner, 1988. *10* – France (Montpellier); Wehner, 1988

Glaessneropsis (0.7% and 0%). The remaining decapods represent (in Saal only) the Homolidae (*Laeviprosopon* – 3%), Dynomenidae (*Oxythyreus* and *Cycloprosopon* – 1.4%), Latreillidae (*Heeia* – 0.7%), Paguridae (*Palaeopagurus* – 0.7%), Axidae (*Magila* – 1%) (Wehner, 1988).

Tithonian

The last Jurassic facies to be discussed is the Tithonian Štramberk-coral-reef (in German literature: Stramberg) one of Tithonian age, extending from the Czech Republic to Romania (Fig. 28). This again represents an episode when prosopids occur in large numbers over a vast area.

Although the known extent of the Štramberk-reef facies is definitely smaller than that of the Oxfordian sponge-megafacies (Fig. 28), an extremely abundant and strongly diversified fauna lived on it, including decapod crustaceans. The Štramberk limestones are present as small klippen-like occurrences in Moravia (Czech Republic), Austria, and Romania, or as olistholites and small exotic fragments in the Cretaceous and Paleogene of the central part of the Outer Carpathians (Czech Republic and Poland). These limestones represent various types of carbonates formed on platforms, developed during the Tithonian along the northern shore of the Tethys or around intrageosynclinal cordilleras, present in the Jurassic Outer-Carpathian basins of the Tethys (e.g., the so-called Silesian cordillera, Baška–Inwałd cordillera – e.g., Książkiewicz, 1956; Krobicki, 1994b; Krobicki & Müller, 1998c).

Corals were the dominant organisms of the Štramberk-reefs. There were mainly phaceloid corals, accompanied by an abundant fauna characteristic of shallow-water environments: the thick-shelled bivalves (*Diceras*), brachiopods, bryozoans, gastropods (*Nerinea*), echinoderms, as well as numerous red algae. Depending on the character of the Štramberk-reef complex, Eliáš & Eliášová (1984) distinguished palaeoenvironmental zones from fore reef through reef core to back reef (lagoon), determining the fauna of these zones. The depth of deposition of the Štramberk limestones was suggested by these authors to be about 15 m or deeper, in the littoral or sublittoral zone of a warm, fairly quiet sea (Morycowa, 1974).

From this limestones Blaschke (1911) described the high diversity assemblage of 607 species, including 34 decapods, of which 9 were prosopids. This abundant crustacean fauna was known already at the end of the 19th century (Moericke, 1889; Remeš, 1895). According to palaeoenvironmental model mentioned above, prosopids preferred probably the reef core, where corals and the robust bivalve *Diceras* prevailed. Prosopids in the exotic blocks of the Štramberk limestones in the Polish Carpathians (Woźniki – Patrulius, 1966; Morycowa, 1974 and Kruhel Wielki – Wójcik, 1914) were found within a very similar faunistic assemblages. This points to the fact that small, vulnerable crabs used the rigid framework of a coral reef as shelter, perhaps living in symbiosis (commensalism?) with the corals in these structure (e.g., *Thecosmilia*, see above: Saal and Stránska Skála Hill). Although coral colonies deformed by crabs nesting within them, as it is the case of the modern corals inhabited by Hapalocarcinidae, or other evidences for commensalism have not been found, a certain level of symbiosis between these animals seems very probable. For the small forms of prosopids living or finding shelter in reef cavities was most probably a defence mechanism against predetors, especially when crabs were loosing their carapaces in moult periods.

In Poland, the Tithonian Štramberk-reef facies is known only from exotic material (olistholites or small exotics) occurring within the Upper Cretaceous–Paleogene strata of the Outer Flysch Carpathians. Patrulius (1966) described the varied fauna of decapods from a large block of the Štramberk limestones in Woźniki (Fig. 28), where *Pithonoton bidentatum* (von Meyer) prevails (39% of the total). The other species include: *P. grande* (von Meyer) (30%), *P. marginatum* (von Meyer) (14.5%), *Longodromites excisus* (von Meyer) (4.3%), and single specimens (1.1% each) of *Nodoprosopon ornatum carpathicum* Patrulius, *Lecythocaris paradoxa strambergensis* Patrulius, and the homolid *Laeviprosopon laeve*. Galatheids represent 8.9% of the whole assemblage of decapods. In the assemblage from Štramberk, Pithonotinae also dominate (Moericke, 1889; Fig. 28), including *Pithonoton marginatum* (Fig. 18 B) (28%), *P. bidentatum* (22%), and *P. grande* (14%).

Klippes of the Štramberk limestones are also known from the Romanian Carpathians: Bucegi Massif (Sinaia and Moroeni), and in Transsylvania, in the eastern part of Postavaru (Keresztényhavas)-Piatra Mare (Nagykő) Massif, at Purcareni (Pürkerec), Satulung (Hosszúfalu), Racos (Felsorákos), Haghimas (Nagyhagymás), and Bicaz Gorge (Békás-szoros), where the decapod crustaceans are well known (Lorenthey & Beurlen, 1929; Patrulius, 1960).

The Tithonian Ernstbrunn limestones are sedimentologically and palaeoecologically similar to the Štramberk limestones; these occur in lower Austria and on the southern slope of the Bohemian Massif of the Jurassic European shelf (Eliáš & Eliášová, 1984; Rehánek, 1987). Bachmayer (1955) collected from these limestones an abundant crustacean material, including four species of prosopids (*Prosopon verrucosum* Reuss, *Pithonoton bidentatum*, *P. grande* and *Longodromites excisus*).

In conclusion, among the Jurassic crustacean decapods the most abundant are the Oxfordian and Tithonian prosopids, which prefer organogenic facies (Oxfordian – sponge, Kimmeridgian – sponge/coral, and Tithonian – coralligenous ones). They belonged, most probably, to Warner's (1977) ethological categories of walking, camouflaging and adapted to commensalism with other organisms.

Upper Cretaceous and Lower Palaeocene

Prosopids were abundant in Upper Jurassic strata, but the subsequent decline of the sponge, coral, or mixed build-ups with which they had been associated, resulted in a scarcity of preserved Cretaceous examples. They are best seen in the Upper Cretaceous of England, described in the monograph of Wright & Collins (1972). Palaeoecological observations are thus limited to this specific material, and a few other occurrences around the world. The species of *Pithonoton*, *Vectis*, *Wilmingtonia*, *Rathbunopon* and *Plagiophthalmus* occur in England mainly in siliciclastic sediments (e.g., Ferruginous Sands of Aptian age; Folkestone Sands of the Upper Aptian). Upper Aptian limestone lenticles also contain an abundant fauna, while crabs can be found in or near nodule beds within the Albian Gault clays of south-eastern England. The sandy Cenomanian deposits yield an exceptionally large crab fauna (Wright & Collins, 1972). The deposits have been sedimented in shallow, wave-affected seas, while local variations in depth could affect the quantity of crab remains, as suggested by these authors. However, the new prosopid species described by Wright (1997), *Rathbunopon*? *atherfieldense* Wright, occur in Lower Greensand (Lower Aptian) of the Isle of Wight (England).

In Spain (Navarre), prosopids (*Rathbunopon obesum* (Van Straelen), *Pithonoton bouvieri* Van Straelen, *P. scara-*

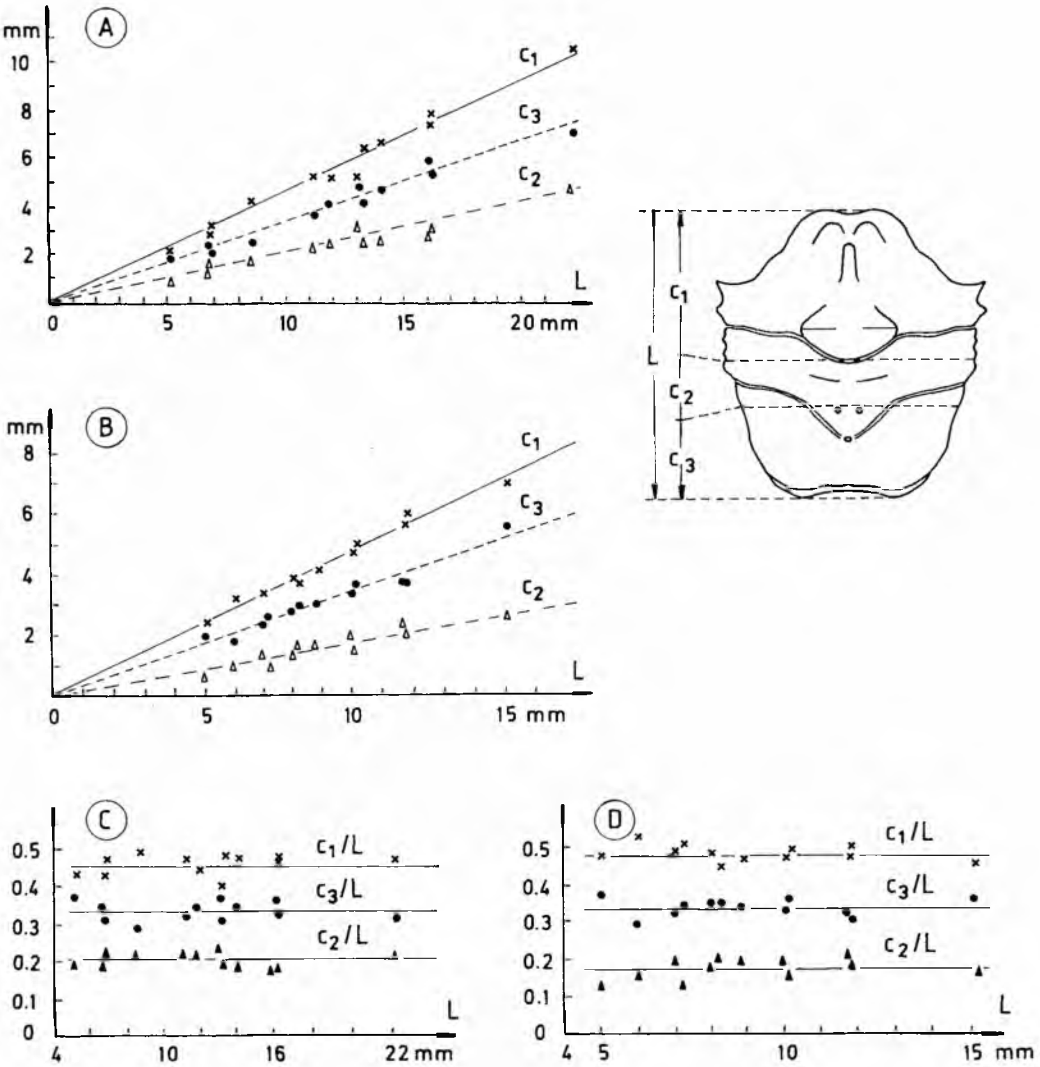

Fig. 29. Ontogenetic variation in carapace length in: **A, C.** *Nodoprosopon spinosum* (von Meyer); **B, D.** *Pithonoton serratum* (Beurlen); Biburg (Germany), Oxfordian (Planula Chron) (after Wehner, 1988)

beum (Wright & Wright), *Plagiophthalmus oviformis* (Bell) and "*Iberihomola*" (?=*Pithonoton*) *laevis* (Van Straelen)), with several other dromiacean and five galatheid species, occur in Cenomanian reefal carbonates (Straelen van, 1940, 1944; Via Boada, 1981; Via & Sequeiros, 1989; Wright, 1997). This indicates a continuation of reef colonisation by prosopids. Additionally, some single specimens of prosopid fauna also occur in limestone boulder within conglomerate (Klement, Lower Austria), which previously was determined as Tithonian species (Glaessner, 1931) (the Klement "Tithonian" crab fauna), recently have been reviewed by Wright (1997) as Cenomanian forms: *Rathbunopon obesum* (van Straelen) and *Pithonoton cenomanense* Wright & Collins. Outside Europe, isolated individual species of prosopid crabs are accessory elements in decapod assemblages. For instance, *Ekalakia lamberti* is present in the decapod-rich assemblages of the famous Cretaceous (Campanian–Maastrichtian) Pierre Shale in eastern Montana and North Dakota (Bishop, 1976; Tucker *et al.*, 1987). Crab *Plagiophthalmus collinsi* Feldmann from the Early Campanian of the Antarctic Peninsula represents the first record of this genus outside Europe and occurs in sandstones "interpreted as having been deposited below storm-wave base in mid to outer shelf depths" (Feldmann *et al.*, 1993: 3).

Summarizing, the Late Cretaceous prosopids, in contrast to the Late Jurassic species, seemed not to prefer any specific sedimentary environment, occurring both in siliciclastic and carbonate sediments. Therefore, they have not been concentrated in one palaeogeographical region with the domination of a specific megafacies, as occured in the Late Jurassic of Europe.

The only known Tertiary (Danian) prosopid, a *Plagiophthalmus depressus* (Segerberg) species (Fischer-Benzon, 1866; Segerberg, 1900; Woodward, 1901; Collins & Jakobsen, 1994), lived on or near by ahermatypic coral colonies on about two or three hundred meters deep bottom (Bernecker & Weidlich, 1990; see bathymetric review – Collins & Jakobsen, 1994).

AUTECOLOGICAL STUDIES

Species of the Oxfordian and Tithonian prosopid crabs are generally small, of similar sizes, and probably possessed similar life cycles as regards their ontogenesis and mortality. Analysis of two species from the Upper Oxfordian of Kraków (Zakrzówek quarry) and from the Franconian Alb (Biburg; cf. Scheirer & Yamani, 1982): *Pithonoton serratum* and *Nodoprosopon spinosum*, showed that these species were characterised by isometric growth during their ontogeny, *i.e.* by a proportional growth of their length and width (Figs 29, 30). Almost all individuals juvenile and adult, were longer than wide. The lack of clearly marked size groups attributable to successive moult stages suggests slow growth between moults. Alternatively, the size ranges of individual moult stages overlaps that of neighbouring stages. Additionally, an unknown impact of sexual dimorphism could further obscure differences between moults. Other arthropods (ostracods, crustaceans, trilobites) show consecutive moult stages preserved in their fossil record, mainly due to well-defined size increases (Shaver, 1960).

Individuals of *Pithonoton serratum* display normal size distribution (Fig. 31), suggesting that the status of a fossil assemblage has been affected neither by heavy early, post-larval mortality nor by massive dying of adult specimens.

Disfigured crabs are generally rare; their proportion is in the range of single percents (1–7%, Houša, 1963). *Pithonoton* and other prosopids often show asymmetrically swollen deformations of the branchial regions (Fig. 17 I, Fig. 18 G). This phenomenon is not limited to brachyuran decapods; e.g., galatheids: *Galathea weinfurteri* Bachmayer (Müller, 1984), *Mesogalathea striata* (Remes) and *Galatheites antiquus* (Moericke) (Boucot, 1990), *Protomunida munidoides* (Segerberg) (Jakobsen & Collins, 1997). Most palaeontologists agree that these deformations result from parasitism of epicaridian bopyrid isopods (Förster, 1969; Glaessner, 1969; Hessler, 1969; Overstreet, 1983; Boucot, 1990; Tucker *et al.*, 1994). Radwański (1972) disagrees with this opinion and suggests that the behaviour of the host (a decapod) to the guest (an isopod) should be interpreted as a commensalism, in view of the fact that swollen branchial regions are found almost only in well developed adult specimens, indicating that isopod growth did not cause the early death of infected specimens. Such deformations have been observed in crabs from the Oxfordian to the recent and is well known both in prosopid crabs: e.g., *Prosopon aculeatum*, *Pithonoton serratum*, *P. marginatum*, *P. bidentatum*, *Nodoprosopon heydeni*, *N. mirum* (Moericke) (Fig. 17 I), *N. ovale* (Moericke), *N. ornatum*, *N. spinosum*, *Longodromites excisus* (Fig. 18 G) (cf. Meyer, 1860; Houša, 1963; Förster, 1969; Radwański, 1972; Wehner, 1988; Boucot, 1990; Conway Morris, 1997), and other brachyurans (e.g., the homolid *Hoplitocarcinus atlantica* (Roberts), the torynommid *Torynomma (Torynomma) australis* Feldmann, the raninids *Cristafrons praescientis* Feldmann and *Notopocorystes stokesii* (Mantell), the goneplacid *Speocarcinus berglundi* Tucker, Feldmann & Powell, the carcineretid *Withersella crepitans* Wrigth & Collins, the xantid *Xanthosia wintoni* Rathbun, and the pinnoterid *Asthenognathus cornishorum* Schweitzer & Feldamnn) (Förster, 1969; Bishop, 1983, 1986a; Boucot, 1990; Feldmann *et al.*, 1993; Tucker *et al.*, 1994; Conway Morris, 1997; Wright, 1997; Hopkins *et al.*, 1999; Schweitzer & Feldmann, 1999). Bopyrid isopod parasites are also known from many recent crabs (e.g., king crab *Paralomis granulosa* infected by a bopyrid species of *Pseudione* – Roccatagliata *et al.*, 1998). In the fossil record we know more dramatically parasitic event, interpreted as castration of the crab *Tumidocarcinus giganteus* Glaessner, probably made by rhizocephalan barnacles (Feldmann, 1998).

BIOGEOGRAPHY

The relative rarity and small size of most fossil decapods and almost all prosopids, makes them inconspicuous to laymen and even to most field geologists. Thus, the prob-

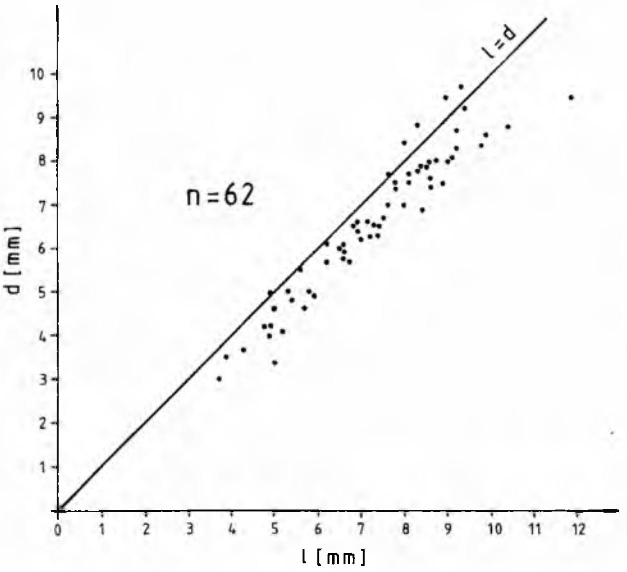

Fig. 30. Ontogenetic variation in carapace length (l) and with (d) in *Pithonoton serratum* (Beurlen); Kraków-Zakrzówek quarry (Poland), Oxfordian (Bimammatum or Planula Chron)

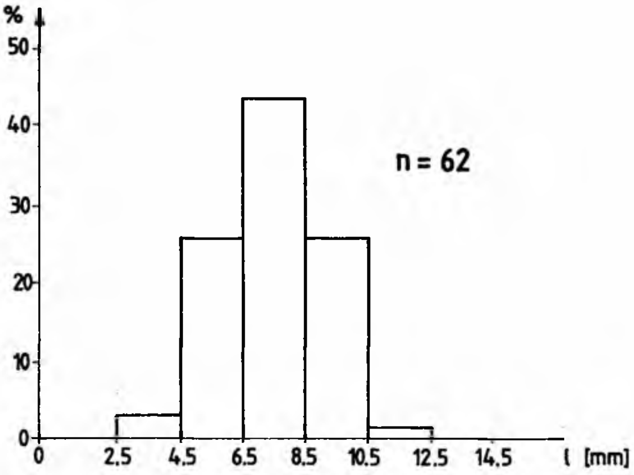

Fig. 31. Size-frequency-distribution of *Pithonoton serratum* (Beurlen) specimens; Kraków-Zakrzówek quarry (Poland), Oxfordian (Bimammatum or Planula Chron)

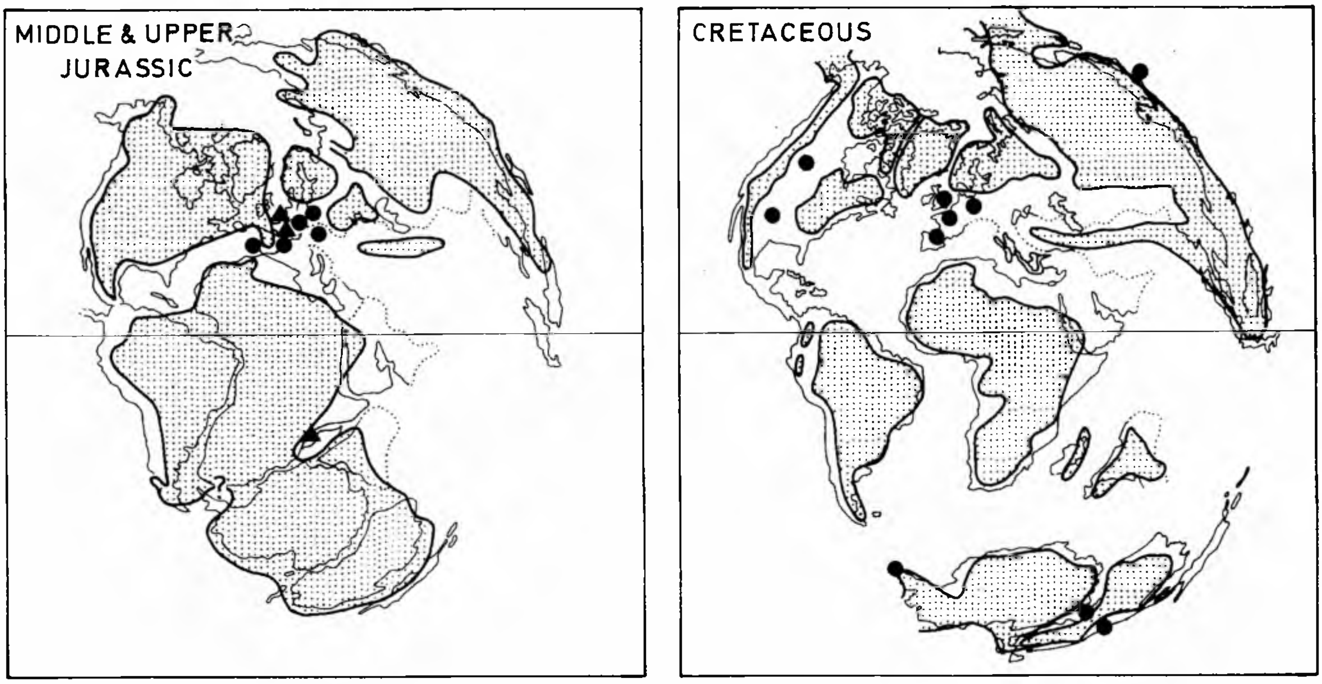

Fig. 32. Palaeogeographic reconstruction showing the distribution of Prosopidae crabs during Middle (triangles) and Late (dots) Jurassic and Cretaceous. Base map from Smith & Briden (1977), coastal lines from Golonka *et al.* (1994)

ability of recognising them is much higher in cases when specialists are collecting. Consequently, most well known decapod localities are clustered around cities containing universities where specialists are present (Müller, 1984), representing a considerable bias in their distributional pattern. This is especially true for Jurassic prosopids where most localities are restricted to a narrow band in Europe, roughly from the Iberian Peninsula to southern Poland and Transylvania, and including Sicily (Fig. 28), where old university cities are more common than in most other parts of the world. The relative rarity of decapod remains explains why they are seldom reported from drill-cores. Thus caution is needed when trying to delineate their palaeogeographic distribution (Bishop, 1986a).

The Mid- to Late Jurassic wide distribution of shallow water environments (maximum a few hundred metres) and in particular the varied reefal habitats around the Tethys Ocean, contributed much to the rapid diversification and success of early crabs (Förster, 1985a). Similarly, the broad expansion of Late Cretaceous shelf seas seems to have contributed to the further evolution of the group.

Two palaeobiogeographical reconstructions (Fig. 32) show the spatial distribution of prosopids from Middle and Late Jurassic to Cretaceous times. Although it was accepted for a long time that Jurassic prosopids occurred in Europe alone, Förster (1985b) reported two Middle Jurassic African species, *Foersteria lugobaensis* (Förster) and *Prosopon* sp., from the Bajocian–Bathonian of Tanzania, indicating that a distribution reached also the southern hemisphere. Most prosopids, however, were found in Europe, although coeval sponge reef-like structures are present in America. The sponge facies of the Smackover Formation in the southern United States is predominantly in subsurface position, known mainly from drill-cores only, making finding of crabs unlikely (Crevello & Harris, 1984). The South American occurrence of such rocks (La Manga Formation of Neuquén Basin, Argentina, cf., Legaretta, 1991) have not yielded decapods either, probably partly due to less extensive collecting (Aguirre Urreta, 1989).

Species of *Pithonoton*, dominating in the Jurassic, are subordinate in Upper Cretaceous deposits, but in turn they may be found outside Europe (Japan, *Pithonoton inflatum* Collins & Karasawa – Collins & Karasawa, 1993), just as are the representatives of *Rathbunopon* (England and Texas, U.S.A.). The crab *Plagiophthalmus collinsi* Feldmann (cf. Feldmann & Wilson, 1988) has been described for the first time outside Europe, viz. from the Campanian of James Ross Basin (the Antarctic Peninsula, Feldmann *et al.*, 1993); being the first known brachyuran decapod from the Cretaceous of the southern part of South America and the Antarctic. Rarity of this occurrence contrasts greatly with the brachyuran-rich assemblages of the Late Cretaceous of North America (cf. the literature in Bishop, 1986a). Another prosopid genus, *Oonoton* (*O. woodsi* Glaessner – Glaessner, 1980) is known from Queensland and South Australia.

Thus, the distribution of the Cretaceous prosopids seems to be much wider than that of the Jurassic representatives (Fig. 32). This may explain why members of the Homolidae (*Homolopsis*), Dynomenidae (*Dromiopsis*) and Torynnommidae (*Dioratiopus*), of which prosopids were probably ancestors (Glaessner, 1980; Via Boada & Sequeiros, 1993), have a world-wide extent.

The only Danian, Early Palaeocene, occurrence of prosopids is in Denmark (Segerberg, 1900; Collins & Jakobsen, 1994). Recently, prosopid-like chelae were found in Lower Palaeocene rocks in Austria as well (Müller, unpublished data).

CONCLUSIONS

Some characteristic patterns may be observed in the palaeoecology of the Jurassic Prosopidae. Prosopid, and, therefore, presumably also brachyuran evolution started in moderately deep, soft bottomed environments. Soon after, the world-wide expansion of epicontinental seas, connected with the Callovian transgression, allowed the formation of bioherms and reefs in the Late Jurassic, creating ideal ecological niches for the rapidly evolving prosopids (Förster, 1985a). When the first Oxfordian cyanobacteria-sponge buildups appeared in Europe, prosopid crabs began to flourish and rapidly occupied these structures in great numbers. These crabs expanded practically all over Europe in the Oxfordian (and perhaps beyond Oxfordian) reflecting the distribution of sponge megafacies from Portugal and Spain to France and, particularly, to Germany and Poland (Fig. 28). From time to time, members of this family frequented also other types of reefal environments (e.g., the Oxfordian coral reef near Brno).

Although there is no evidence for soft bottom dwelling prosopids during Late Jurassic times, their presence may not be ruled out, considering the general scarsity of decapods in sediments deposited in such environments. However, a massive and diverse existence of crabs in Late Jurassic to Early Cretaceous soft bottom environments seems to be highly unlikely. The distribution of known Prosopids shrank in the Kimmeridgian, as the sponge-coral facies declined except everywhere in southern Germany (Leinfelder, 1993). In turn, a regression in the peri-Tethyan area during the latest Jurassic resulted in changes of habitats and in colonisation of the Štramberk coral reefs along the northern margin of the Tethys, where these crabs probably reached a climax (Fig. 28) (Krobicki & Müller, 1998a, b, c).

The abundant and diverse reefal crab associations, as compared with soft bottom asssociations, probably reflects both the high diversity and abundance of crabs living on reefs and their elevated preservational potential in this environment.

It is clear, though, that early primitive crabs preferred shallow marine environments (some tens to a few hundred metres) with bioherms or reefs, *i.e.* sponge and sponge-coral reefs in the Oxfordian–Kimmeridgian as well as coral reefs in the Tithonian of the northern Tethyan ocean. The structure of the Late Jurassic decapod associations differed in time and space, as summarised below.

The Oxfordian assemblages were dominated by *Pithonoton serratum* (Germany – 57%; central Poland – 70%; southern Poland – 69%). Thus, the sub-family Pithonotinae definitely prevails over the Prosopinae in faunal assemblages (Fig. 28). The galatheid *Gastrosacus wetzleri* dominated in the Kimmeridgian, for which the coral reefs of the Franconian and Schwabian Alb represented an favourable environment. This species composed up to half of the specimens of an assemblage (Saal – 49%). Thus, even in the relatively short time between the Oxfordian and Kimmeridgian, a sudden change in decapod crustacean assemblages took place as the result of the ecological transition from sponge bioherms to coral reefs. However, similar situation occurred in the Tithonian (Štramberk limestones – coralineous facies) and in the Oxfordian (sponge facies): Pithonotinae again were dominant, with few representatives of galatheids (Fig. 28). Both the Oxfordian cyanobacterial-sponge bioherms and Štramberk coral reefs represented better habitats for prosopids than the Kimmeridgian coral-reefs, within which the prosopids were partly replaced by galatheids. Prosopids were more opportunistic than anomurans. In all Late Jurassic assemblages discussed, homolids, mainly *Laeviprosopon laeve*, occur as accessory components.

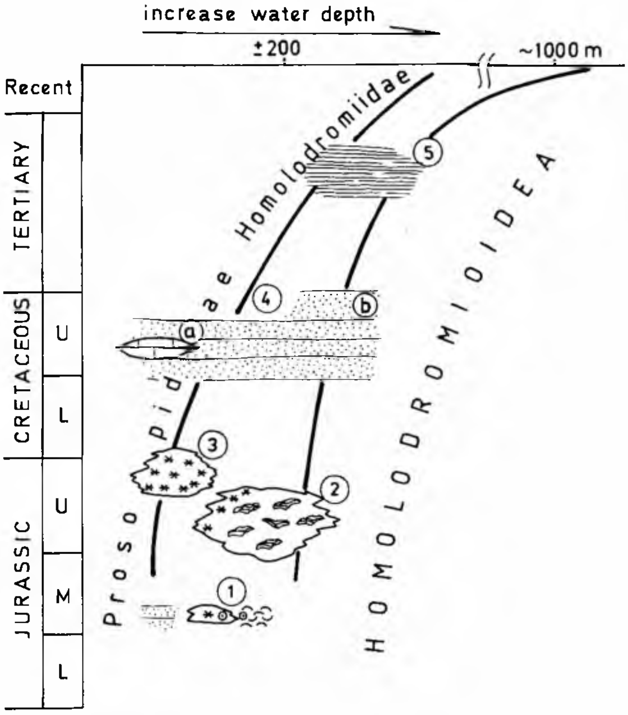

Fig. 33. Trend of environmental displacement of Homolodromioidea crabs from Jurassic to Recent based on palaeo- and ecological preferences of fossil and extant taxa. *1* – Middle Jurassic environments: shallow-water siliciclastic and carbonate (coral reefs, crinoid limestones, brachiopod shell beds) deposits; *2* – Oxfordian cyanobacteria-sponge and sponge-coral buildups; *3* – Tithonian Štramberk coral reefs; *4* – Upper Cretaceous shallow water siliciclastic (a – with limestone lenses) and outer shelf (b) environments; *5* – Tertiary outer shelf deposits

As long as the cavity-bearing (rigid framework) Late Jurassic organic buildups were present, delicate prosopid crabs could find a refuge from predators and the abundance of nutrients in such environments facilitated food gathering and survival. Migration of prosopids to the margins of the Tethyan ocean took place in the Late Jurassic by the regression of epicontinental seas and reef-like structures disappeared within the peri-Tethyan basins. The isolated occurrences of Late Jurassic prosopids outside the centres of a "reef" sedimentation suggest that this fauna adapted poorly to non-reefal palaeoecological conditions.

When biohermal and reef facies retreated at the Jurassic–Cretaceous boundary, favourable conditions for prosoponid crab development decreased, so that known Cretaceous prosopids are rare and spatially dispersed. Thus, prosopids had their climax during Late Jurassic time with a wide distribution in the sponge and coral reef environments of Europe, probably developed under tropical and subtropical conditions in shallow, warm waters. Their closely related descendants, the homolodromiids, preferentially inhabited soft muddy bottoms in deeper, colder waters. Such ecological displacement to deeper habitats (Fig. 33) is well documented by Tertiary fossils (e.g., *Homolodromia chaneyi* Feldmann & Wilson, or *Antarctidromia inflata* Förster, which probably lived in deeper, outer shelf environments) and recent ones (e.g., Atlantic and Carribean *Homolodromia paradoxa* Milne-Ewdards or *H. bouvieri* Doflein – ranges through depth 650–960 metres, and Indo-West-Pacific or Atlantic *Dicranodromia*) (cf. Förster *et al.*, 1987; Feldmann & Wilson, 1988; Feldmann & Gaździcki, 1998; see also Feldmann *et al.*, 1991; Collins, 1997). Some homolodromiids actually live even deeper than 1000 m (e.g., *Dicranodromia mahyeuxi* Milne-Edwards, Förster *et al.*, 1987, or *Homologenus broussei* Guinot & Forges, Guinot & Forges, 1981).

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Streszczenie

JURAJSKIE I KREDOWE PRYMITYWNE KRABY Z RODZINY PROSOPIDAE (DECAPODA: BRACHYURA) – ICH TAKSONOMIA, EKOLOGIA I BIOGEOGRAFIA

Pál Müller, Michał Krobicki & Gabriele Wehner

W pracy przedstawiono diagnozę systematyczną wszystkich rodzajów krabów z wymarłej rodziny Prosopidae (Decapoda: Brachyura) podając ich zasięgi stratygraficzne (Fig. 1), zilustrowano typowe gatunki (Fig. 2–18) oraz przeanalizowano przypuszczalne powiązania filogenetyczne z innymi rodzinami krabów jurajskich i kredowych (Fig. 19–22). Na podstawie kolekcji własnych i muzealnych przeprowadzono analizę paleoekologiczną i przedstawiono biogeograficzne rozprzestrzenienie przedstawicieli tej jednej z najstarszych kopalnych rodzin prymitywnych krabów.

Dało to możliwość prześledzenia paleośrodowiskowych preferencji jurajskich krabów i zmiany warunków życia ich potomków z młodszych linii rozwojowych.

Nasza wiedza o wczesnych, jurajskich krabach jest skąpa i oparta głównie na nielicznych znaleziskach. Chociaż, ilość żyjących dzisiaj krabów ocenia się na około 4500 gatunków (Warner, 1977), znajomość ich wczesnych protoplastów jest ograniczona. Wynika to głównie z bardzo niskiego potencjału fosylizacyjnego tych skorupiaków. Niemal każde znalezisko kopalnych krabów jest w związku z tym bardzo ważne dla paleontologii i może służyć w rozwiązywaniu zagadnień tafonomicznych, paleobiologicznych czy filogenetycznych. Kraby, które za życia miały cienką kutykulę, trudniej ulegają fosylizacji w porównaniu z innymi stawonogami jak trylobity, których zapis paleontologiczny jest o wiele obfitszy ze względu na silnie wapienny pancerz. Słaby zapis kopalny tej grupy jest dodatkowo skutkiem związku większości taksonów ze ściśle określonymi facjami i z tego powodu obszar ich występowania jest ograniczony. Świadczą o tym przykłady europejskich jurajskich prosoponów (opisany w niniejszej pracy oryginalny materiał z górnej jury Polski i Niemiec), gdzie geologiczny kontekst ich występowania umożliwia rekonstrukcję paleoekologicznych zależności.

Oszacowano destrukcyjny wpływ procesów tafonomicznych (dysartykulacja, transport, chemiczne rozpuszczanie i biologiczna dekompozycja pancerzy) na możliwość i jakość zapisu w zespole kopalnym pierwotnych populacji. Możliwością uniknięcia negatywnych skutków takich procesów było szybkie tempo pogrzebania pancerzy, powstanie wokół rozkładającego się ciała miękkiego konkrecji mineralnych (syderyty, fosforyty) (Baird *et al.*, 1986) lub schronienie się w norach penetracyjnych. Ta ostatnia możliwość była wykorzystywana zarówno przez liczne raki (por. Bromley & Assgard, 1972) jak i kraby (np. Richards, 1975; Förster *et al.*, 1987). Jednak jak do tej pory nie znaleziono wśród jurajskich prosoponów przykładów takiej strategii etologicznej. Wydaje się więc, że jedyną szansą na zachowanie fragmentów tych krabów było szybkie pogrzebanie ich pancerzy po śmierci, szczególnie w osadzie, który nie był później bioturbowany. W oparciu o kolekcję z utworów oksfordu i tytonu z obszaru Polski, w porównaniu z innymi, głównie trzeciorzędowymi formami, autorzy proponują schematyczny model przedstawiający zależność procesów tafonomicznych od czynników biologiczno-sedymentologicznych (Fig. 23). Wydaje się, że najistotniejsze znaczenie biostratynomiczne ma zróżnicowanie natężenia bioturbacji w osadzie gdzie znajdują się świeżo pogrzebane szczątki krabów i ich mikrobiologiczna dekompozycja (Plotnick, 1986). Przy wzroście natężenia tych czynników szansa dobrego zachowania się tych szczątków w zapisie kopalnym gwałtownie spada. Mogą one doprowadzić do całkowitej eliminacji pancerzy z tanatocenozy.

Z obserwacji współczesnych środowisk jak i interpretacji paleośrodowisk późnojurajskich wynika, że najskuteczniejszym mechanizmem obronnym przed destrukcyjnym wpływem środowiska, zarówno fizycznego jak i biologicznego było kamuflowanie się w obrębie raf lub struktur rafopodobnych. Współcześnie takie zjawiska są znane na dużą skalę (Wells, 1960; Warner, 1977; Prahl, 1983; Bishop, 1986). Niektóre z krabów używają innych organizmów do kamuflażu. Spektakularnym przykładem jest krab gąbkowy (*Cryptodromia hilgendorfi* – daleki potomek jurajskich prosopidów) żyjący u wybrzeży Australii, który wykorzystuje głównie gąbki z rodzaju *Suberites*, będąc z nimi prawdopodobnie w komensalizmie (McLay, 1982, 1983). W zapisie kopalnym liczne są przykłady wykorzystywania budowli organicznych (rafy, biohermy, biostromy) przez skorupiaki dziesięcionogie (Yanakevitch, 1969; Müller, 1984; Förster, 1985a).

Spośród jurajskich dziesięcionogów najliczniejsze są oksfordzkie i tytońskie prosopony, które preferowały facje organogeniczne (oksford – gąbkowa, tyton – koralowa). Kraby te należały najprawdopodobniej do etologicznej kategorii Warnera (1977), krabów chodzących, kamuflujących się i przystosowanych do komensalizmu z innymi organizmami.

Wszystkie do tej pory opisane gatunki środkowojurajskich Prosopidae pochodzą ze środowisk płykomorskich. Najstarszy znany gatunek tej rodziny – *Eoprosopon klugi* (późny pliensbach) żył prawdopodobnie tak samo jak pierwszy znany prawdziwy krab *Eocarcinus praecursor* (młodsza część wczesnego pliensbachu) na piaszczystym dnie. Tryb życia mógł być podobny do etologii ich bezpośrednich przodków (Pemphicidae) jako zwierząt również płytkowodnych, mięso-, roślino- bądź padlinożernych. Analiza facji, fauny towarzyszącej i warunków paleogeograficznych sugeruje, że środkowojurajskie prosopony żyły w płytkich, ciepłych wodach w obrębie węglanowych facji organogenicznych (Francja, Tanzania, Niemcy, Austria) (Förster, 1985b).

Ogólnoświatowa transgresja kelowejska i związane z nią szerokie rozprzestrzenienie się w późnej jurze biohermalnych i rafowych struktur gąbkowych, gąbkowo-koralowych lub koralowych w Europie, ułatwiła bardzo silny i gwałtowny rozwój rodziny Prosopidae (Förster, 1985a). Takie budowle węglanowe stały się idealnymi ekologicznymi niszami dla tych drobnych krabów. Już nigdy później w geologicznej historii tej rodziny nie doszło do tak obfitego jej rozkwitu zarówno pod względem ilości gatunków jak i osobników.

Szeroko rozprzestrzeniona w całej Europie megafacja gąbkowa oksfordu dostarczyła najbardziej licznej fauny prosoponów. Zarówno w Jurze Polskiej jak i Jurze Frankońskiej i Szwabskiej (Niemcy), pierwsze liczne prosopony występują w małych biohermach (do kilku metrów średnicy) cjanobakteryjno-gąbkowych środkowego (Polska) lub górnego (Niemcy) oksfordu, które w obydwu przypadkach znajdują się w obrębie wapieni płytowych jako izolowane biostruktury (por. Szklarka i Biburg – Fig. 24–27). Biohermy zbudowane przez gąbki krzemionkowe charakteryzowały się sztywnym szkieletem podczas swojego wzrostu (Matyszkiewicz, 1994, 1997). Jest bardzo charakterystyczne, że kraby i pojedyncze krewetki występują wyłącznie w tych małych, izolowanych biohermach, podczas gdy w otaczających je wapieniach płytowych skorupiaki reprezentowane są tylko przez raki z rodzaju *Glyphea* (Fig. 26). Podobne obserwacje poczyniono w obrębie utworów oksfordu na obszarze Jury Polskiej i południowo-zachodnim obrzeżeniu Gór Świętokrzyskich, gdzie liczna fauna krabów (głównie prosoponów z rodzajów: *Prosopon*, *Pithonoton*, *Nodoprosopon*) została opisana z wapieni typu gąbkowego (Collins & Wierzbowski, 1985), podczas gdy izolowane pancerze raków *Glyphea* znaleziono w wapieniach płytowych interpretowanych jako środowiska położone na zewnątrz lub pomiędzy biohermami cjanobakteryjno-gąbkowymi (Förster & Matyja, 1986). Całkiem nowe są znaleziska szczątków krewetek, które występują tylko w wapieniach biohermalnych. Prawdopodobnie małe prosopony i krewetki wykorzystywały biohermy gąkowe jako ochronę przed potencjalnymi drapieżnikami, na które były narażone, zwłaszcza tuż po zrzuceniu pancerza w procesie linienia. Biohermy te ułatwiały im przeżycie stwarzając możliwość schronienia się w licznych próżniach wzrostowych, w które biohermy były obfite, w przeciwieństwie do otaczającego je miękkiego mułu węglanowego. Ten drugi był z kolei zasiedlany przez nieliczne raki, które dzięki swoim długim odnóżom preferowały ten typ dna. One prawdopodobnie były producentami nor typu *Thalassinoides* (Hoffmann & Uchman, 1992). W interpretacji autorów ścisła zależność między krabami, krewetkami i lokalnie obfitymi gąbkami jest odbiciem komensalizmu (0+) pomiędzy tymi zwierzętami, gdzie dla fauny skorupiaków gąbki były niezbędne do przeżycia (+), a gąbkom ich obecność była obojętna (0) (por. Ager, 1963).

W późnym oksfordzie okolic Krakowa zanikła facja wapieni płytowych a powstawały wapienie masywne (skaliste) i uławicone. Liczne kraby występują wewnątrz próżni wzrostowych wapieni gąbkowych a wraz z nimi ramienionogi (*Terebratulina substriata*) i serpule. Kraby z rodziny Prosopidae występują obficie głównie w wapieniach uławiconych, gdzie masowo występują gąbki oraz inna fauna bentoniczna (zwłaszcza ramienionogi, głównie z rodziny Dallinidae i małże). Środowisko sedymentacji tych wapieni jest interpretowane jako między- lub pery-biohermalne (por. Merta, 1972; Nitzopoulos, 1973).

W Europie w utworach kimerydu prosopony występują prawie wyłącznie na terenie Jury Frankońskiej i Szwabskiej (rodzaje: *Prosopon*, *Pithonoton*, *Nodoprosopon*, *Longodromites*, *Lecythocaris*, *Glaessneropsis*) początkowo w obrębie masywnych wapieni gąbkowych a później gąbkowo-koralowych i koralowych (Meyer, 1975; Meyer & Schmidt-Kaler, 1990). Te ostatnie budują głównie korale z rodzaju *Thecosmilia*, *Dermosmilia*, *Ovalastrea* czy *Calamophyliopsis*. Kraby są niekiedy znajdowane w obrębie labiryntowych struktur w skupiskach masywnych korali *Thecosmilia*, gdzie prawdopodobnie ukrywały się one przed drapieżnikami (por. Wehner, 1988).

Ostatnim epizodem któremu towarzyszyła obfitość krabów Prosopidae na dużym obszarze jest tyton. Co prawda zasięg facji sztramberskiej jest zdecydowanie mniejszy niż megafacji gąbkowej w oksfordzie, bo ograniczony tylko do łuku karpackiego i platformy mezyjskiej (por. Fig. 28), ale dostarczyła ona bardzo licznej i silnie zróżnicowanej fauny – w tym skorupiaków dziesięcionogich. W wielu miejscach Europy środkowej znajdują się dzisiaj wystąpienia tych wapieni (Czechy, Polska, Rumunia). W Polsce jest ona znana wyłącznie z materiału egzotykowego (olistolity i egzotyki), które występują obecnie w obrębie górnokredowo-paleogeńskich utworów Karpat fliszowych. Wapienie typu sztramberskiego reprezentują różne typy litofacjalne platform węglanowych rozwiniętych w tytonie przy północnym brzegu Tetydy i wokół śródgeosynklinalnych kordylier "egzotykowych" egzystujących w zewnętrznokarpackim, jurajskim basenie Tetydy (np. kordyliera śląska, kordyliera Baśka–Inwałd) (Książkiewicz, 1956; Krobicki, 1994). Zespół organizmów z koralowcami, gruboskorupowymi małżami (*Diceras*), ramienionogami i amonitami zawiera również liczne dziesięcionogi, z dominującymi prosoponami (*Pithonoton*, *Longodromites*, *Nodoprosopon*, *Lecythocaris*) (Moerick, 1889; Remeš, 1895; Patrulius, 1966).

Migracja prosoponów do marginalnych, północnych partii oceanu Tetydy w tytonie w poszukiwaniu najlepszych warunków środowiskowych determinowana była pod koniec jury regresją mórz epikontynentalnych i związanym z tym zanikiem facji rafopodobnych w ich obrębie. Izolowane wystąpienia późnojurajskich Prosopidae poza centrami "rafowej" sedymentacji świadczą dodatkowo o małej zdolności przystosowania się tej fauny do innych warunków paleośrodowiskowych.

Do niedawna jeszcze jedynym znanym obszarem występowania jurajskich Prosopidae był teren Europy. Jednak obecność gatunku *Foersteria lugobaensis* w jurze środkowej (bajos lub baton) Tanzanii, wskazuje, że już w jurze środkowej ich zasięg obejmował również półkulę południową, powiększając tym samym potencjalne centrum ewolucji krabów (Förster, 1985a). Późnojurajskie środowiska sedymentacji rafowej spowodowały skupienie się przedstawicieli Prosopidae na terenie Europy, chociaż rafopodobne struktury gąbkowe znajdują się w tym czasie zarówno w Ameryce Północnej (np. formacja Smackover w Stanach Zjednoczonych – Crevello & Harris, 1984) jak i Południowej (formacja La Manga basenu Neuquén w Argentynie – Legaretta, 1991). Jak dotychczas jednak w regionach tych nie znaleziono do tej pory fauny skorupiaków.

Kredowi przedstawiciele rodziny Prosopidae, w przeciwieństwie do gatunków późnojurajskich, nie preferowali żadnego konkretnego środowiska sedymentacji, występując zarówno w obrębie utworów klastycznych jak i węglanowych. Dlatego nie są one skupione w jednym regionie paleogeograficznym, gdzie dominuje określona megafacja, jak miało to miejsce w późnej jurze w Europie (por. Fig. 32).

Analizę autekologiczną przeprowadzono na materiale pochodzącym z górnego oksfordu okolic Krakowa i Jury Frankońskiej obejmując nią gatunki: *Pithonoton serratum* oraz *Nodoprosopon spinosum*. Obydwa gatunki charakteryzują się izometrycznym wzrostem podczas ontogenezy (Fig. 29, 30). Podczas wzrostu prawie zawsze długość osobników była większa od szerokości i ta reguła potwierdza się zarówno u osobników juwenilnych jak i dorosłych. Brak wyraźnie zaznaczonych stadiów wylinkowych sugeruje, że wzrost krabów w okresach kiedy były one pozbawione twardego pancerza był bardzo powolny, przez co poszczególne stadia wylinkowe nie różniły się zmianami proporcji ciała. Z drugiej strony jest możliwe, że osobniki tego samego stadium wylinkowego mogły się na tyle różnić rozmiarami, że duże osobniki wcześniejszego stadium wylinkowego mogły być większe od małych osobników stadium późniejszego. Dodatkowo nieznany wpływ dymorfizmu płciowego na różnicę rozmiarów pomiędzy osobnikami żeńskimi a męskimi mógł zatrzeć różnicę pomiędzy wylinkami. W niektórych wypadkach w obrębie innych skorupiaków (małżoraczki, trylobity) w zapisie kopalnym zachowały się poszczególne stadia wylinkowe, głównie dzięki gwałtownym skokowym przyrostom ciała (Shaver, 1960).

Histogram rozkładu wielkości osobników gatunku *Pithonoton serratum* przedstawia rozkład normalny (Fig. 31), co sugeruje, że na stan zespołu kopalnego nie miała wpływu ani wczesna, polarwalna śmiertelność ani masowa śmiertelność dorosłych osobników. Na osobnikach rodzaju *Pithonoton* najczęściej zachowały się asymetryczne wybrzuszenia regionu oskrzelowego, wywołane przez zasiedlenie się bopyridowych równonogów (Isopoda) w oskrzelach dziesięcionoga (Boucot, 1990) (Fig. 17 I, Fig. 18 G). Ilość krabów tak zniekształconych jest w populacjach zazwyczaj niska i wynosi kilka procent (Houša, 1963). Przez większość paleontologów tego typu deformacja pancerza uznawana jest jako rezultat pasożytnictwa równonogów (por. Förster, 1969; Boucot, 1990; Tucker *et al.*, 1994). Odmiennego zdania jest Radwański (1972), który sugeruje, że stosunek gospodarza (dziesięcionóg) do gościa (równonóg) należy interpretować jako komensalizm ze względu na fakt, że deformacje te występują tylko u osobników dorosłych i dobrze wyrośniętych co z kolei wskazuje, że rozwój równonoga nie prowadził do śmierci "zainfekowanego" osobnika. Wśród krabów kopalnych takie deformacje znane są u form od oksfordu do późnego pliocenu.

Po obfitym występowaniu w utworach górnej jury krabów Prosopidae, zanik na przełomie jury i kredy węglanowych budowli gąbkowych, koralowych i mieszanych, z którymi one były związane, spowodował że znaleziska kredowych przedstawicieli rodziny są rzadkie i izolowane. Najlepiej zostały one poznane na podstawie materiału paleontologicznego z kredy (alb–cenoman) Anglii (Wright & Collins, 1972). Gatunki z rodzaju *Pithonoton*, *Vectis*, *Wilmingtonia*, *Rathbunopon* czy *Plagiophthalmus* występują w Anglii głównie w utworach klastycznych, a podrzędnie w wapiennych soczewkach w ich obrębie. Środowiska sedymentacji tych utworów wskazują na płytkie, ruchliwe morza, chociaż lokalne zmiany głębokości mogły wpływać na obfitość szczątków krabów (Wright & Collins, 1972). W innych miejscach w Europie prosopony znajdowane są w węglanowych facjach pochodzenia rafowego (cenoman Hiszpanii) (Via Boada, 1981). Pojedyncze gatunki tej rodziny znajdowane poza Europą są akcesorycznymi elementami zespołów kopalnych (np. *Ekalakia lamberti* – Bishop, 1976; *Plagiophthalmus collinsi* – Feldmann *et al.*, 1993).

Dominujące w jurze gatunki rodzaju *Pithonoton*, w utworach górnej kredy występują rzadko, ale za to spotykane są również poza Europą (np. Japonia), podobnie jak przedstawiciele rodzaju *Rathbunopon* (Ameryka Północna) czy pierwszy poza Europą gatunek rodzaju *Plagiophthalmus* (Antarktyka). Rozprzestrzenienie kredowych gatunków rodziny Prosopidae w porównaniu z jurajskimi taksonami jest zatem o wiele szersze, ale znane są one tylko z pojedynczych znalezisk. Z tego powodu ogólnoświatowy zasięg mają przedstawiciele Homolidae (*Homolopsis*), Dynomenidae (*Dromiopsis*) czy Torynommidae (*Dioratiopus*), dla których kraby Prosopidae były przodkami (Glaessner, 1980; Via Boada & Sequeiros, 1993). Najbliżsi potomkowie rodziny Prosopidae – kopalni przedstawiciele rodziny Homolodromiidae – zasiedlili środowiska miękkiego dna głębszych i zimniejszych mórz, co jest zarówno dobrze udokumentowane paleontologicznie w utworach trzeciorzędu jak i potwierdzone współczesnymi badaniami gatunków tej rodziny (Fig. 33).