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HOMOLODROMIID CRABS FROM THE CAPE MELVILLE FORMATION (LOWER MIOCENE) OF KING GEORGE ISLAND, WEST ANTARCTICA
(Plates 36—43)


More than 280 remains morphologic of the crabs Antarctidromia inflata FÖRSTER, 1985 have been collected from the Lower Miocene Cape Melville Formation of King George Island (South Shetland Islands, West Antarctica). The excellent preserved specimens allow a detailed analysis. The pattern of the carapace shows closer relationships to Jurassic Prosopidae from the Bathonian than to the two Recent genera: Homolodromia and Dicranodromia. A. inflata appears to have been adapted to a low-energy environment cool and deep water on the outer shelf in high latitudes.

Key words: Homolodromiid crab, taxonomy, paleoecology, Lower Miocene, South Shetland Islands, Antarctica.

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KRABY HOMOLODROMIDOWE Z OSADÓW FORMACJI CAPE MELVILLE (DOLNY MIOCEN) WYSPY KRÓLA JERZEGO, ANTARKTYKA ZACHODNIA

Streszczenie. — Praca jest taksonomicznym studiem krabów z gatunku Antarctidromia inflata FÖRSTER, 1985. Bogata kolekcja licząca ponad 280 okazów pochodzi z lodowcowo-morskich osadów dolnomicoceńskiej formacji Cape Melville na Wyspie Króla Jerzego (Szetlandy Południowe, Antarktyka Zachodnia). Doskonały stan zachowania pancerzy krabów pozwolił na ich szczegółową analizę morfologiczną i porównanie z kopalnymi i współczesnymi przedstawicielami rodziny Dromiidae. Wykazują one większe podobieństwo do najstarszych przedstawicieli Prosopidae znanych z batonu niż do współcześnie żyjących z rodzajów Homolo-
INTRODUCTION

Crab-rich locality — the Crab Creek, discovered on King George Island in the South Shetland Islands archipelago by Polish field party during the 1980—1981 austral summer, provided a collection of over 280 specimens of first Tertiary homolodromiid crab (GAŻDZICKI and WRONA 1982, FORSTER et al. 1985).

Glacio-marine sediments of the Cape Melville Formation which yield studied homolodromiid crabs occur in the easternmost part of King George Island, the Melville Peninsula (fig. 1). The Cape Melville Formation (up to 200 m thick) is represented by fossiliferous marly shales with siltstones, marls and sandstones intercalations. This sequence which also yielded ice-rafted dropstones of Antarctic landmass provenance, gives evidence a continental glaciation called the Melville Glaciation (BIRKENMAJER 1982, 1984, 1987 this volume). The radiometric K-Ar data (around 20 Ma) obtained from the two andesite dykes cutting through glacio-marine sediments of the Cape Melville Formation allow to estimate the age of the formation as not younger than the Early Miocene (BIRKENMAJER et al. 1985). Taking into account that the Destruction Bay Formation which underlays the Cape Melville Formation yielded the Early Miocene brachiopod fauna, an Early Miocene age is suggested for the Cape Melville Formation and the Melville Glaciation (BIERNAT et al. 1985, BIRKENMAJER et al. 1985).

The field work in Antarctica was undertaken during the Fifth Polish Antarctic Expedition 1980—1981 led by Professor K. BIRKENMAJER.

The collection of crabs is housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warszawa, Poland (abbreviated as ZPAL).

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MATERIAL AND MODE OF PRESERVATION

The homolodromiid crabs of the species Antarctidromia inflata and crab burrows occur in marly shales of the upper part of the Cape Melville Formation exposed on the top of the peninsula plateau in the Crab Creek area (fig. 1). Associated fossils include diatoms (mostly centric), radiolarians, chrysomonads, agglutinated and calcareous benthic foraminifers, numerous solitary corals (Flabellum), bryozoans, bivalves, gastropods, scaphopods, polychaetes, ostracods, echinoids and a few fish remains. This Tertiary fossil assemblage is an autochthonous biota often occurring in live orientation (GAŻDZICKI and WRONA 1982, BIRKENMAJER et al. 1983, see also RONIEWICZ and MORYCOWA 1985, 1987 this volume; KARCZEWSKI 1987 this volume, SZANIAWSKI and WRONA 1987 this volume, JESIONEK-SZYMAŃSKA 1987 this volume). Furthermore occur recycled fossils include Cretaceous calcareous nannoplankton (DUDZIAK 1984) and belemnites (BIRKENMAJER et al. 1987, this volume).

The studied crab collection consists of approximately 200 nearly complete or almost complete carapaces and 80 fragments as abdominal segments, appendages or chelae (pls. 36—41; Fig. 9). Most specimens of Antarctidromia inflata found in situ are preserved in a life-
Fig. 1
Location of the Melville Peninsula in King George Island and Crab Creek on the Melville Peninsula. Dotted areas show distribution of the Tertiary rocks of the Moby Dick Group (modified from Birkenmajer 1982). A — Polish Antarctic Station Arctowski.
like attitude with the dorsal parts uppermost, the chelipeds folded ventrally against the buccal cavity and the ambulatory legs in a walking arrangement. Although many carapaces are slightly crushed, most are remains of dead animals rather than moults. Carapaces, external and internal skeletons and sutures had been weakened by post-mortem decalcification and deformed early diagenetically during compaction of the enclosing sediment. The most perfectly preserved specimens occur within compact marly limestone concretions which formed within the sediment. Crab remains appear to have served as nuclei for diagenetic processes producing the concretions. Most intensive cementation occurred in the ventral regions of the crabs, particularly around the abdomen, the pleural sutures and proximal to the joints of the appendages. Sediments enclosing the dorsal parts of the carapace or the chelae are weakly cemented. Stronger calcified regions with less pores and natural openings for diffusion, remained less cemented than regions with many sutures. Weakly calcified parts, favoured better chemical interchanges between decomposing organic material and enclosing sediment. Cementation however increases dorsally with increasing amount of crushing. Remains preserved in shales and marls are usually less complete and often heavily crushed. Not only the carapaces, but even the appendages have then been deformed dorsoventrally.

Many specimens of *Antarctidromia inflata* have a remarkably well-preserved cuticle (pl. 42: 1). External cuticles are black to brownish, in weathered specimens commonly bluish white or brownish white. In thin sections they are brown to amber. Examined with the scanning electron microscope the cuticle reveals a gross structure similar to that of extant decapods. A thin unlamellated layer is probably equivalent to the epicuticle of living decapods. The main layer is finely laminated (pl. 42: figs. 1—3) and is equivalent to the calcified zone of the endocuticle. Occasionally it contains small clusters of pyrite, particularly in vugs (pl. 42: 4).

Only a few specimens show distinct indications of decomposition and transport: mostly the ventral skeleton with the appendages had been shifted, but rarely more than half of the width of the carapace and always laterally (ZPAL Cr. 1/60, 96, 122). In one dislocated concretion (ZPAL Cr. 1/127) carapace and abdomen are juxtaposed. The abdomen rotated approximately 180° around the carapace (pl. 37: 6). There are few examples of clustered assemblages. In few cases crabs *Antarctidromia* and the corals *Flabellum* were found together. These few examples, as well as disintegrated specimens and even single, isolated appendages, are rare (< 20%), in comparison with other occurrences of fossil decapods. This may be the result of selective fossilization as well as selective collecting related to different weathering of fossils from shales or concretions on the eroded bedding-plane. In summary, all fossil components display little or no post-mortem disturbance reflecting an in situ faunal association. The life-like positions of many fossil crabs suggest rapid burial, perhaps induced by storm-generated fine-grained sediment (see discussions below).

**PALEOECOLOGICAL REMARKS**

The life-like attitude of many specimens of *Antarctidromia* indicates that these animals were already buried while still alive. The occurrence in spheroidal and ellipsoidal concretions is the result of decomposition of the dead animals, entombed in the sediment. The sub-cylindrical burrows are associated with the crabs and they often weather out on the flat lying bedding-plane and erosional surface on the top of the Melville Peninsula (pl. 43: 1). The burrows are usually subcircular in transversal section (pl. 43: 2—3) and 3—10 cm wide and up to 100 cm long. They are more or less straight or gently curved, somewhat widening towards the end (pl. 43: 5—6). The burrows form mainly horizontal tunnels in the bedding-plane without branching or arrangements in galleries (pl. 43: 1). Occasionally a crab was found within a burrow
Fig. 2
Relation of length ($C_l$) and width ($C_{br}$) of carapace of 109 measured specimens; note gradual change in shape to wider carapaces in larger individuals.

(plt. 43: 4). The association of crabs with burrows may indicate that the crabs are autochthonous or paraautochthonous relics of an ancient community.

The biology of Recent Homolodromioidea is insufficient known to indicate whether the burrows definitively represent dwelling structures which the animals maintained and occupied or if the burrows served simply as occasional refuge, particularly during the vulnerable soft-shelled phase after moulting. The numerous remains of Antarctica without any relationship to burrow structures, however, as well as the absence of distinct moults suggest that these crabs may have lived in semi-permanent burrows or that they have been able to rapidly bury themselves for protection in soft muddy bottoms as known from closely related Recent Dromiidae.

The suggestion that the crabs are relics of ancient communities is strengthened by the occurrence of apparently all growth stages, from juvenile individuals of only 25 mm length to adults of about 99 mm length (fig. 2). But there is an evident preponderance of carapaces less than 50 mm length. Furthermore there seems to be a notable inequality in the ratio of males to females. According to the narrow shape of nearly all observed abdomens, males seem to be
more abundant than females. Females should show more broadly oval abdomens for the protection of the eggs, as known from Recent crabs. Unfortunately, in no specimen the genital openings have been observed at the coxae of the third to fifth pereiopods. Minor differences in the shape of the abdomen appear in specimens which are longer than 50 mm (fig. 3). The differences increase with size, but do not reach an obvious bimodal frequency distribution. In Recent crabs a clearly bimodal distribution is realized only in communities of adult individuals. Only 22 specimens (8%) have carapace and abdomen sufficiently preserved. Detailed morphologic analysis of the total fauna and comparison with Recent homolodromiid crabs suggest, that the fauna represents a life assemblages of juvenile and half-grown individuals. The occurrence of solitary corals preserved in life position in the same bedding-plane, may indicate an in situ life assemblage, buried suddenly by a blanket of sediment.

All Recent Homolodromioidea inhabit preferably soft muddy bottoms in deeper water of at least 150 m depth. *Dicranodromia mahyeuxi* MILNE-EDWARDS for example, has been dredged from more than 1100 m depth. The abundance of ahermatypic corals of the genus *Flabellum* LESSON therefore is of particular interest as a depth indicator (RONIEWICZ and MORYCOWA
Comparable to the ecological displacement of the homolodromiid crabs since Cretaceous times, the Caryophyllidae show a resembling retreat to bathyal environments and to higher latitudes since Jurassic times (Wells 1967). Recent species of the genus *Flabellum* range from shallow water to more than 3000 m depth (Wells 1967, see also Roniewicz and Morycowa 1987, this volume), often with narrow depth limits for a single species. But the distribution of Recent ahermatypic corals is much more controlled and limited by the temperature of the water at the bottom than by depth (Wells 1967). The common occurrence of glacially-striated erratic blocks (up to 2 m in diameter), interpreted as iceberg-rafted dropstones (Birkenmajer et al. 1983) points to a cold water environment in high latitudes. The association of crabs, ahermatypic corals, and the whole biotic assemblage suggests a deeper outer shelf environment.

**SYSTEMATIC DESCRIPTION**

Subsection *Dromiacea* De Haan, 1833  
Superfamily *Homotodromioidea* Alcock, 1899  
Genus *Antarctidromia* Förster, 1985  
*Antarctidromia inflata* Förster, 1985  
(pls. 36-41; figs. 2-8)

Material. — Over 280 specimens (ZPAL Cr. 1/1—280).

Measurements (in mm):

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<tr>
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<th>L</th>
<th>W</th>
<th>L/W</th>
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<td>46</td>
<td>1.07</td>
<td>22</td>
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<td>31</td>
<td>1.07</td>
<td>15</td>
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<td>21</td>
<td>20</td>
<td>1.05</td>
<td>9.7</td>
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L — length of carapace measured from exorbital tooth to posterior margin; W — width of carapace; LG — length of gastric region (= distance exorbital tooth — median cervical groove).

Description. — Carapace longer than wide (L/W 1.07, see fig. 2), pear-shaped with greatest width and height in posterior third. Dorsal surface moderately convex, bent downwards anteriorly. Sharp lateral margin, starting from exorbital tooth (ES) and expiring on posterior part of branchial region.

Frontal region narrow, cut into three teeth: a pair of strong preorbital (lateral frontal) spines (PrS) and a median frontal spine (FS). Frontal spine directing obliquely downwards, preorbital spines upwards/outwards (figs. 4—6). Preorbital spines on outer edge armed by minute spines (fig. 4). Narrow antennoorbital cavity, dorsally protected by frontal (FS), preorbital (PrS) and a minute exorbital spine (ES), ventrally by a small infraorbital spine (IS) and epistome (ep) (fig. 6).

Carapace widening from exorbital tooth (ES) which corresponds with the antero-external angle of the buccal cavity. Anterolateral margin concave in outline with two spines: a small
Antarctidromia inflata FÖRSTER; terminology of carapace regions and grooves: a branchiocardiac groove, ae attachment area of attractor epimeralis muscle, AS antennal spine, ee cervical groove, EB epibranchial region, EBI epibranchial lobe, ES exorbital tooth, FS frontal spine, H hepatic lobe, HS hepatic spine, md median dorsoventral muscle, MsG mesogastric lobe, MsB mesobranchial region, MtB metabranchial region, pc posterior cardiac marking, PG protogastric lobe, pgp posterior gastric pits, PrS preorbital spine, U urogastric region.

Antennal spine (AS) about half between exorbital (= supraorbital BALSS 1940) and the prominent hepatic (anterolateral spine IHLE, 1913) (HS) at the anterolateral angle of carapace. Two small bosses just behind hepatic spine, anterior of cervical groove. Carapace posterior the branchiocardiac groove significantly widening, forming a more or less symmetrical convex arch to posterior margin. Posterior margin sinuare.

Cervical (ee) and branchiocardiac (a) grooves well developed. Both grooves cross lateral margin and join with antennal (b) and hepatical (b,) groove. A zone of weakness (l) accompanies the grooves ventrally, ascending backwards against the lateral margin and expires on the posterior branchial region. It may be comparable to the linea dromica of Recent Dromiidae. Cervical groove with posterior gastric pits (pgp). Conspicuous lateral gastrocardiac (ae), median dorsoventral (md) and posterior cardiac (pc) markings.
Mesogastric lobe (MsG) flattened, epi/protogastric lobes (EG, PG) inflated. Pronounced bosses on posterior protogastric (PG) and hepatic (H) lobes, arranged on a transverse line with hepatic spine (HS) approximately parallel with cervical groove (ee). Inflated bilobed urogastric region (U). Depressed narrow cardiac region (C), expanded and inflated posterior into an equilateral triangle. Triangle ornamented by small bosses at each apex. A weak longitudinal ridge runs from the cervical groove into the cardiac region. Epibranchial region (EB) bounded by cervical (ee) and branchiocardiac (a) grooves and gastrocardiac markings (ae). Mesobranchial (MsB) and metabranchial (MtB) regions confluent, gently convex with a slight kidney-shaped elevation parallel to posterior cardiac markings (pc). Depressed intestinal region (I) with a pair
of weak, backwards diverging ridges. Subhepatic region (SH) flattened to depressed, ventral upturned into a marginal rim along antennal (b) und cervical (ee.) grooves and divided by another approximate vertical rim into two areas (fig. 5).

Entire surface of carapace ornamented by small granules except for grooves and markings. Posterior branchial region with some single tubercles.

Abdomen infolded against sterna. First two segments visible from dorsal side. Both reduced in breadth to allow a dorsal position of the last two pereiopods. Well developed pleura, distinctly delimited from the median arch of the tergum. Second an especially sixth somite lengthened (fig. 7). Sixth somite without marginal „intercalar plates” developed in the Dromiidae or Dynomenidae. Large subtriangular telson.

Thoracic sterna 1 to 3 fused to a narrow triangular projection (fig. 8). Median bosses as remnants of somite boundaries. Posterior-lateral projections (episternum) (est_s₃₋₆) form the ventral supports for the articulation of the third maxillipeds and pereiopods. In sterna 4—6 transverse grooves as remnants of somite boundaries.

Third maxillipeds (Mxp₃) cover mouth parts in buccal cavity; subpediform and strongly calcified. Basis and ischium fused; long, and rounded-triangular in cross-section. One outer and two inner edges. Ventral edge armed by strong spines (fig. 7).

First pereiopods with chela. Ambulatory legs with dactyli only. Last two pereiopods with subchela, probably for covering the carapace with sheltering objects as Recent Dromia-cea use to do. Fourth and fifth pereiopods reduced in size to about half of the length of
Antarctidromia inflata Förster; sternum; thoracic sterna 1 to 3 fused to a narrow triangular projection; median bosses as remnants of somite boundaries; posteriolateral projections ("episternum") form the ventral supports for articulation of Mxp₃ and pereiopods; transverse grooves as remnants of somite boundaries in somite 4 to 6; est₃-₆ episternum 3 to 6, Mxp₅ third maxilliped, Pp₄-₅ pereiopods 1 to 3.

**Remarks.** — The closest relationships show some recently discovered homolodromiid crabs from the Late Eocene (La Meseta Formation) of Seymour Island, east of James Ross Island, West Antarctica (Feldmann 1985 written communication). There are close relationships to some of the oldest Prosopidae as Prosopon mammillatum (Woodward) and P. au-duuni (Deslongchamps) from the Bathonian. The carapaces of these prosopids show a pattern of differentiation close to that of Antarctidromia (Förster et al. 1985, fig. 4). The two extant genera Homolodromia and Dicranodromia show less similarities.
Antarctidae *infusa* Förster; reconstruction.
REFERENCES


EXPLANATIONS OF THE PLATES 36—43

All specimens are from the Cape Melville Formation (Lower Miocene), King George Island, West Antarctica

PLATE 36

Antarctidromia inflata FÖRSTER, 1985

1—2. Dorsal and ventral view of a larger individual with well preserved third maxillipeds; ZPAL Cr. I/1, natural size.
3. Lateral view of carapace; note prominent hepatic spine; ZPAL Cr. I/63, natural size (compare pl. 37, fig. 2 and pl. 41, fig. 5).
4. Dorsal view of carapace; hepatic and particularly branchial region crushed by compaction of the sediment; ZPAL Cr. I/3, \( \times 1.5 \).
5. Dorsal view of small individual; ZPAL Cr. I/5, natural size.

PLATE 37

*Antarctidromia inflata* Förster, 1985

1. Frontal view; downwards directed frontal spine (FS); preorbital spines (PrS) broken off. Right cheliped folded downwards; ZPAL Cr. I/139, \( \times 2 \) (compare fig. 5 below).
2. Frontal view showing frontal spine, preorbital spines and flattened subhepatic region below frontolateral margin and antennal (AS) respectively hepatic (HS) spines; ZPAL Cr. I/63, \( \times 2 \) (compare pl. 36, fig. 3; pl. 41, fig. 5).
3. Carapace of small individual with proximal parts of the last two pereiopods; ZPAL Cr. I/5, natural size (compare pl. 36, fig. 5 before preparation).
4. Individual showing parts of the right pereiopods: cheliped folded ventrally against buccal cavity; ZPAL Cr. I/17a, natural size.
5. Individual with downwards folded right cheliped (compare fig. 1 above); ZPAL Cr. I/139, natural size.
6. Disintegrated individual; ventral skeleton with attached proximal parts of pereiopods and abdomen have been rotated 180° around the carapace, lying sideward above carapace; abdomen partly disintegrated and inflexed; ZPAL Cr. I/127, natural size.

PLATE 38

*Antarctidromia inflata* Förster, 1985

1. Dorsal view of large individual, showing second pereiopod (ischium and merus) in a life-like position; note spine lateral margin of left preorbital (PrS) spine; ZPAL Cr. I/7, natural size.
2. Largest carapace of *Antarctidromia*; ZPAL Cr. I/6, natural size.

PLATE 39

*Antarctidromia inflata* Förster, 1985

1. Lateral view of a small crushed specimen; ZPAL Cr. I/52, natural size.
2. Individual in life-like attitude; ventral skeleton slightly dislocated to the left side; the first two somites of the abdomen are visible; holotype ZPAL Cr. I/4, \( \times 1.5 \).
3. Dorsal view of heavily crushed carapace; ZPAL Cr. I/2, \( \times 1.5 \).
4. Individual in life-like attitude; fifth pereiopods reduced in size and shifted in a subdorsal position; ridges of pereiopods armed by strong spines; ZPAL Cr. I/44, natural size.
CRABS FROM THE CAPE MELVILLE FM.

PLATE 40

Antarctidromia inflata Förster, 1985

1. Frontolateral view of frontal region, showing downwards directed frontal spine, antennooorbital cavity and proximal parts of right antennula (a2); ZPAL Cr. 1/233, x 4.
2. Lateral view of carapace showing lateral margin which expires on posterior branchial region; ZPAL Cr. 1/2 (see pl. 39, fig. 3), x 1,5.
3. Ventral view of disintegrated individual, showing the life-like position of chelipeds; ZPAL Cr. 1/85, natural size.

PLATE 41

Antarctidromia inflata Förster, 1985

1. Disintegrated ventral skeleton; note the narrow anteromedian projection (= fused thoracic sterna 1 to 3) and the posterolateral projections of sterna 3 to 5 (= episternum) which support the articulation of the third maxillipeds and the pereiopods; ZPAL Cr. 1/18, natural size.
2. Ventral view of individual showing the abdomen, proximal parts of pereiopods 1 to 3 and remains of the third maxillipeds; ventral skeleton slightly shifted to the left side; ZPAL Cr. 1/3, natural size (compare pl. 36, fig. 4).
3. Ventral view of holotype; note life-like position of pereiopods; merus of the second pereiopod lengthened in relation to the merus of the cheliped; ZPAL Cr. 1/4, x 1,5.
4. Abdomen and proximate parts of pereiopods 1 to 3; ZPAL Cr. 1/13, natural size.
5. Dorsal view of carapace showing well preserved frontal region; preorbital spine (PrS) with delicate lateral spines, prominent hepatic (HS) spine; ZPAL Cr. 1/63 (compare pl. 36, fig. 3; pl. 37, fig. 2), natural size.
6. Abdomen and proximate parts of pereiopods 1 to 4; note the well developed pleura, distinctly deliminated from median arch of the tergum; ZPAL Cr. 1/24, natural size.

PLATE 42

Antarctidromia inflata Förster, 1985

1. Cuticle; vertical break showing unlamellated layer (at the top, right) probably equivalent to the epicuticle, and the finely laminated calcified zone of the endocuticle, x 200.
2. Enlargement of part of fig. 1; x 500.
3. Enlargement of central part of fig. 2; x 1400.
4. Small clusters of pyrite in vugs of the laminated layer; x 2000.

All figures are SEM micrographs

PLATE 43

1. Horizontal burrow from the upper part of the Cape Melville Formation, exposed on the top of peninsula plateau in the Crab Creek area.
2-3. Transversal sections of the burrow; ZPAL Cr. 1/281; natural size.
4. Transversal section of burrow enclosing crab carapace; pereiopods arrowed; ZPAL Cr. 1/282; natural size.
5. Burrow, showing lower surface; visible internal structure; ZPAL Cr. 1/283; x 0,7.
6. General view, of the top surface of a burrow; ZPAL Cr. 1/284; x 0,5.
R. Förster, A. Gażdzicki and R. Wrona: Crabs From The Cape Melville Fm.
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