

## LATE EOCENE CORAL-ASSOCIATED DECAPODS (CRUSTACEA) FROM HUNGARY

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Fifty-eight species of fossil crabs are recorded and figured from Facies 4, a coral-bearing limestone, of the Szépvölgy Formation (Late Eocene, Priabonian) of Hungary. The following 18 genera, 1 subgenus and 35 species are new: *Dardanus curtimanus*, *Pagurus latidactylus*, *Diogenes longimanus*, *Paguristes oligotuberculatus*, *Galathea* (*Acanthogalathea* subgen. nov.) *parva*, *Protomunida pentacantha*, *Longoporcellana denticulata* gen. nov., *Polyonyx arcuatus*, *Petrolisthes* ? *striatissimus*, *Ovocarcinus elongatus* gen. nov., *Dromilites fossata*, *Dromilites subglobosa*, *Kromtitis pentagonalis*, *Cymonomus primitivus*, *Ovamene franciae* gen. nov., *Ethusa evae*, *Gemmacarcinus fossatus* gen. nov., *Nanomaja simplex* gen. nov., *Mesolambrus declinatus* gen. nov., *Actaeites lobatus* gen. nov., *Paraxanthosia budensis* gen. nov., *Pilumnomimus planidentatus*, *Priabonocarcinus gallicus* gen. nov., *Prochlorodius ellipticus* gen. nov., *Sculptoplax rigida* gen. nov., *Eomaldivia pannonica* gen. nov., *Eomaldivia trispinosa*, *Budapanopeus denticulatus* gen. nov., *Panopeus granulineatus*, *Branchioplax sulcata*, *Caprocancer altus* gen. nov., *Corallicarcinus planus* gen. nov., *Daragrapsus trispinosus* gen. nov., *Eoplax minima* gen. nov., and *Palaeograpsus bitneri*. Another new genus, *Lobogalenopsis* gen. nov., is introduced to accommodate a previously described species and eight species in as many genera are described, but not named.

Key words — Crustacea, Decapoda, Late Eocene (Priabonian), Hungary, new taxa.

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### INTRODUCTION

The Priabonian (Late Eocene) Szépvölgy Limestone Formation (Hofmann, 1871) includes layers of several facies of limestones, marls and clastic rocks. Three of these (nos 4, 5 and 6 in text-fig. 1) yield decapod remains. The sequence is a typically transgressive one for which Kázmér (1985) proposed a

model. In the present paper we describe the decapod fauna collected from the 4-5 m thick coral-bearing limestones of Facies 4. Kázmér (1985, p. 143, MF-6A) described the microfacies of this limestone. Kolosváry (1949) enumerated the corals originating from this layer; the most abundant genus is *Actinacis* d'Orbigny, 1849, often with vertically-standing branches, and colonies of *Goniopora* de Blainville, 1840, *Astreopora* de Blainville, 1830, *Alveopora* de Blainville, 1830 and ? *Leptomussa* d'Achiardi, 1867. Colonies seem to 'float' in the matrix, their position being stabilised mainly by the accumulating sediment. Kázmér (1985, p. 143) interpreted his observations as follows, "calm, well oxygenated environment below wave base. The

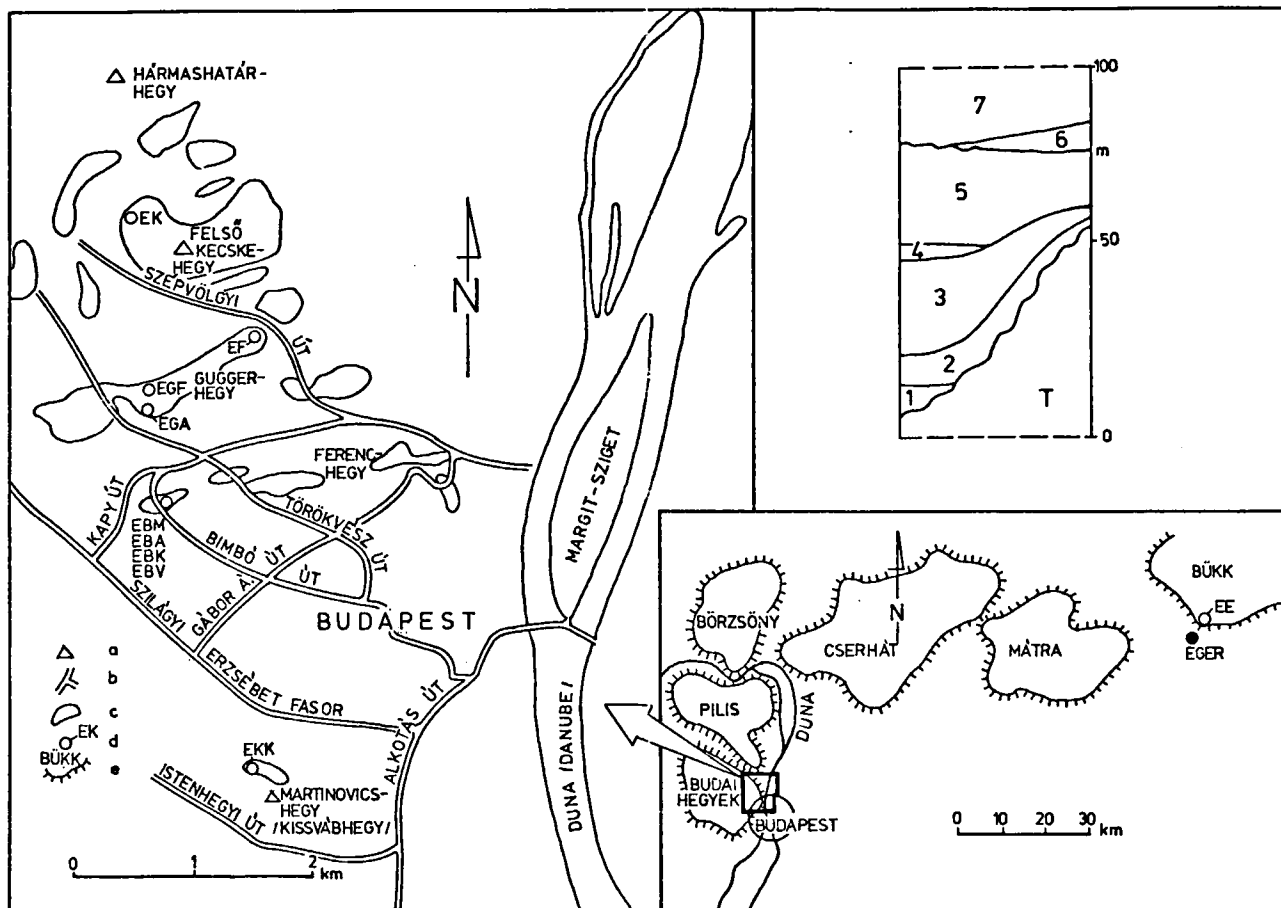


Fig. 1. Localities of decapods from Facies 4 of the Szépvölgy Limestone, and facies diagram of the Szépvölgy Limestone in the Buda hills:

- a - summits;
  - b - main streets;
  - c - outcrops of Szépvölgy Limestone in the Buda area;
  - d - Facies 4 of:
    - EKK, 2-3 m thick hard limestone with corals, Martinovics-hegy (Kissvábhegy), northern quarry, partly infilled leaving Facies 4 no longer accessible.
    - EB, different types of coral-bearing rocks, succession and thickness unknown, from the foundations of house, 185 Bimbo út.
    - EBA, hard limestone with branching colonies of ahermatypic corals.
    - EBK, hard limestone with *Actinacis*.
    - EBM, marly limestone with *Actinacis*.
    - EBV, unidentified limestone.
    - EF, blackish and dark grey limestone with *Astreopora* and *Goniopora* from the uppermost 0.5 m thick part of a 4 m thick coral-bearing layer in an abandoned quarry, the so-called Francia-Kőfejtő.
    - EGF, marly limestone with *Astreopora*.
    - EGA, marly limestone blocks scattered in woodland covering the west foot of Gúggerhegy.
    - EK, a 4 m thick layer of hard limestone, with a slightly marly intercalation, with several species of coral, mainly *Actinacis*, from an abandoned quarry, Ruprecht Kőfejtő, Felső Kecse-hegy.
    - EE, Eger, blocks of hard algal limestone scattered over the summit of the hill, Kis-Eged-hegy (described in Lőrenthey & Beurlen, 1929, p. 82).
  - e - mountains, high hilly areas
- T - cliffs of Carnian dolostone, karstified; Facies are as follows: 1 - terrestrial, variegated clays, silts and gravel; 2 - aprons of abrasional breccia, conglomerate; 3 - calcirudite, coarse calcarenite; 4 - coral limestone, Facies 4 as described in the text; 5 Ícalcarenite with discocyclinids; 6 - marl with bryozoans; 7 - Buda Marl Formation. Facies 2-6 belong to the marine Szépvölgy Limestone Formation, the thickness of which varies from 10-100 m; Facies 1 is Priabonian or older; Facies 2-7 are Priabonian in age.

branching corals attenuated water motion near the sediment base, so micritic mud was deposited and bound by red algae ... The 5 m thick bed at Fenyőgyöngye with corals in micritic mud can be interpreted as a coral-algal mud-mound". Such conditions might prevail in open seas of several tens of metres depth, or in lagoons of several metres depth.

The Szépvölgy Limestone is rather lithified, hard and stylolitic partly due to an overburden of about 1000 m and partly by hydrothermal activity (Müller, in press).

*Previous studies of the Szépvölgy Limestone* — Lórenthey (1897, 1898a, 1898b, 1898c, 1901a, 1901b, 1904a, 1904b, in Lórenthey & Beurlen, 1929) studied the decapod fauna of the Szépvölgy Limestone. Most of his fauna was collected from Kissvábhegy (now Martinovicshegy, text-fig. 1) from Facies 4, 5 and 6, and from Szépvölgy (Facies 5), and a few specimens originated from other Budapest localities; Eger (Facies 4) and from Urhida (Facies 5). From Lórenthey's descriptions and from an examination of the matrix of preserved specimens we have prepared a list of the fossil content of the individual facies, based on Lórenthey's posthumous publication in Lórenthey & Beurlen (1929).

-Facies 4: *Galathea (Palaeomunida) defecta* (Lórenthey, 1901), *Cyamocarcinus angustifrons* Bittner, 1883, *Daira eocaenica* (Lórenthey, 1897), *Phlyctenodes krenneri* Lórenthey, 1897, *Phlyctenodes steinmanni* Lórenthey, 1901, *Titanocarcinus kochii* Lórenthey, 1897, *Laevicarcinus egerensis* Lórenthey, 1929, *Neptocarcinus millenaris* Lórenthey, 1897, *Neptocarcinus spinosus* Lórenthey, 1897 [= *Coralliocarcinus spinosus* (Lórenthey, 1897)], *Galenopsis similis* Bittner, 1875, *Galenopsis quadrilobatus* Lórenthey, 1897 [= *Lobogalenopsis quadrilobata* (Lórenthey)], *Daranyia granulata* Lórenthey, 1901.

-Facies 5: *Callianassa pseudofraasi* Lórenthey, 1929, *Callianassa glabra* Lórenthey, 1929, *Callianassa spinosa* Lórenthey, 1897 (= *subspinosa* Glaessner, 1929), *Rhachiosoma* sp. [= *Ctenocheles* sp.], *Noetlingia claudiopolitana* (Bittner, 1893), *Dromilites pentagonalis* (Lórenthey, 1929) [= *Pseudodromilites* sp.], *Laeviranina simplicissima* (Bittner, 1883), *Laeviranina budapestiniensis* (Lórenthey, 1897), *Lophoranina bittneri* (Lórenthey, 1901), *Lophoranina reussi* (Woodward, 1866), *Lophoranina marestiana avesana* (Bittner, 1883), *Notopus beyrichi* Bittner, 1875, *Ranilia vareolata* (Lórenthey, 1929) [= *Notopella vareolata*], '*Typilopus*' *semseyanus* Lórenthey, 1929, *Calappilia dacica* (Bittner, 1893), *Micromaiia tuberculata* Bittner, 1875, *Periacanthus horridus*

Bittner, 1875, *Phrynelambrus corallinus* Bittner, 1893, *Portunites ? eocaenica* Lórenthey, 1929, *Titanocarcinus elegans* Lórenthey, 1929 [= *Montezumella elegans*], *Titanocarcinus raulinianus* (A. Milne Edwards, 1865), *Palaeocarpilius macrochelus coronatus* (Bittner, 1886), *Palaeograpsus loczyanus* Lórenthey, 1897, ? *Phlyctenodes hantkeni* Lórenthey, 1897, '*Hepaticus*' *laevis* Lórenthey, 1929 — these last two species may originate from Facies 4.

-Facies 6: *Calappilia dacica* Bittner, 1893, *Micromaiia punctulosa* Lórenthey, 1929 [= *Pisomaia tuberculata* Lórenthey, 1929], *Titanocarcinus raulinianus* and *Lobocarcinus paulinowuerttembergensis* von Meyer, 1851. Dr Tibor Kecskemeti kindly studied Lórenthey's only specimen of the last-named species and confirmed (pers. comm.) the Kissvábhegy origin from the nummulitid foraminifera in the matrix. Lórenthey's study was based on material collected partly by himself, partly by geologists, amateurs and quarrymen; since Lórenthey & Beurlen (1929) only one short paper (Müller, 1975) has dealt with decapods of the Szépvölgy Limestone.

*Localities and methods of collecting* — The present work is based on material collected mainly by one of us (P.M.) during the last 30 years in abandoned quarries and on natural outcrops or road cuts (text-fig. 1). There has been limited quarrying in Kecskemeti (text-fig. 1) and Martinovics-hegy (text-fig. 1) during the past 40 years, but work has now entirely ceased in the area. Fieldwork was carried out with the aid of head-band magnifying glasses which facilitated the recognition of specimens down to 2 or 3 mm in size. Methods for extracting the specimens were described in Müller (1984a, p. 35).

#### SYSTEMATICS

Our material consists of detached carapaces and chelae. Carapace morphology, for the moment, seems insufficient for arranging Eocene species in modern families as currently widely recognised. Especially significant is the old family Xanthidae which is now split into numerous smaller families. For this reason we adopt Glaessner's (1969) system, although even here a separation of Xanthidae from Goneplacidae for Eocene species seems sometimes problematical for several genera, e.g. *Titanocarcinus*, or for the newly introduced *Coralliocarcinus*.

Almost all of Lórenthey's material survives and is kept in the Magyar Állami Földtani Intézet (MÁFI), Budapest, XIV Népstadion út 14. That part of our material, indicated by letters and numbers (e.g.

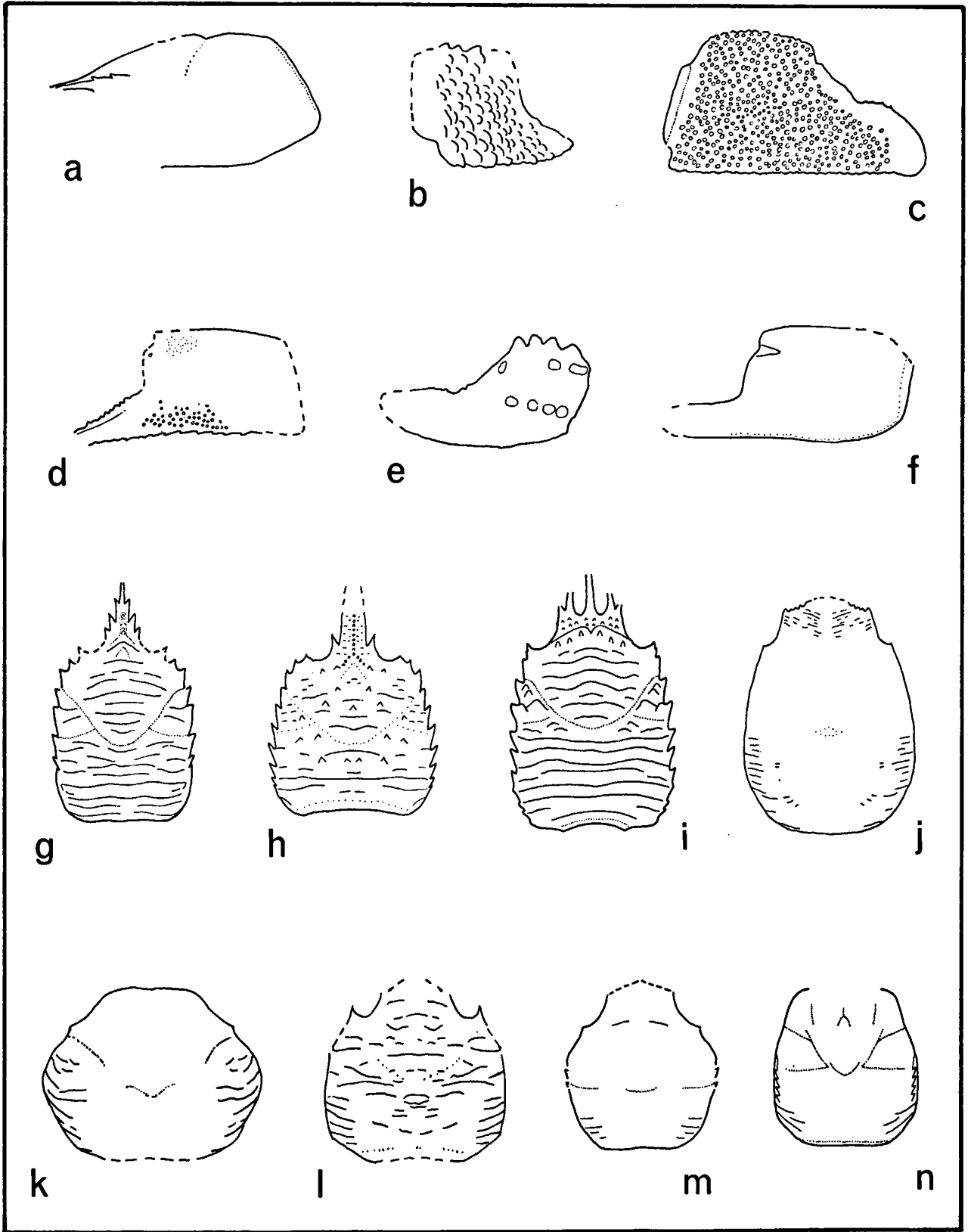


Fig. 2. Diagrammatic views of: a - Homarinae ? sp., b - *Dardanus curtimanus* sp. nov., c - *Pagurus latidactylus* sp. nov., d - *Diogenes longimanus* sp. nov., e - *Paguristes oligotuberculatus* sp. nov., f - *Anapagurus* sp., g - *Galathea (Palaeomunida) defecta* (Lorenthey), h - *Galathea (Acanthogalathea) parva* subgen. et sp. nov., i - *Protomunida pentacantha* sp. nov., j - *Longoporcellana denticulata* gen. et sp. nov., k - *Polyonyx arcuatus* sp. nov., l - *Petrolisthes ? striatissimus* sp. nov., m - Porcellanidae sp. A, n - Porcellanidae sp. B.

EF-13.2 — where the letters indicate the locality, the numbers the species' serial number, while the number of individuals comes after the point) is kept in the collection of P.M.; it is now deposited in the Természettudományi Múzeum, Föld-és őslénytar, VIII Múzeum krt. 14-16, H-1088 Budapest, and the registration numbers are given in square brackets (e.g. M.91-97).

The type locality and type stratum for all new species is: Budapest, Late Eocene, Priabonian. More precise definition of the localities is given in the code numbers of the holotypes (see text-fig. 1).

Infraorder Astacidea Latreille, 1803  
 Family Nephropsidae Dana, 1852  
 Subfamily Homarinae Huxley, 1879

Homarinae ? gen. et sp. indet.  
 Pl. 1, Figs 1, 3; text-fig. 2a

*Material* — Fragments of posterior parts of two carapaces; the external mould of an anterior part and an almost complete right propodus of the cheliped (EF-33.1-4 [M.91-97]). The fragments may well represent several species, but similarity in size suggests their common identity.

*Description* — A deep cervical groove, V-shaped in dorsal view, crosses the upper one third of the carapace. Other furrows are absent or rudimentary. The dorsal margin is arched, slightly V-shaped. A long rostrum is visible on the fragment representing the anterior part of the carapace, the rostral margin appears to be entire although its preservation is moderate; it continues onto the carapace as a ridge bearing at least two small teeth. The chela is elongated, the manus quite stout, widening distally and there are traces of tubercles distally. The opposing margin of the dactylus is sharp with numerous fine teeth, of which the proximal ones are the largest, the tip forms a hook-like, upturned prolongation.

*Discussion* — The fragments most probably belong to a new reptant macruran form; their fragmentary preservation, however, casts doubts on their specific identity and preclude formal taxonomic classification.

Infraorder Anomura H. Milne Edwards, 1832  
 Superfamily Paguroidea Latreille, 1802  
 Family Paguridae Latreille, 1802

*Remarks* — Using some, often superficial, morphological similarities we have placed five species into five

extant genera of the family Paguridae. These names may reflect either remote relationships or homoeomorphies, in both cases they should be regarded as collective taxa.

Genus *Dardanus* Paulson, 1875

*Type species* — *Dardanus hellerii* Paulson, 1875, by monotypy. Range: Eocene-Recent.

***Dardanus curtimanus* sp. nov.**

Pl. 1, figs 4-6; text-fig. 2b

1975 '*Pagurus*' sp. — Müller, pp. 516, 520.

*Derivation of name* — Alluding to the short manus. *Material* — Holotype, a left propodus, EK-6.1 [M.91-99]; paratype, a right propodus EF-5.1 [M.91-98].

*Description* — The short propodus is quite convex, thick and in lateral view it converges distally. The length of the manus is about six sevenths of the maximum height and it is elliptical in cross-section. The fixed finger is stout, wide, with the cutting surface depressed. The surface ornament of the chela is better preserved on the paratype and consists of vertically elongated tubercles which tend to be arranged in vertical rows which are rather wider proximally, narrowing distally; there are about ten on the lower edge of the manus. There were probably another four or five rows on the fixed finger, but these are obscured by poor preservation. On the upper margin of the manus are three or four large blunt tubercles, partly broken down and visible only as prints on the external mould.

*Discussion* — The species shows remote similarities to the extant *Dardanus callidus* (Risso, 1827) being similarly covered with tubercles, although the arrangement of the tubercles is different and the manus is stouter and shorter in the Eocene form. The three Miocene species, described in part by Lórenthey & Beurlen (1929) and assigned to this genus by Müller (1984a) differ from the Eocene one in having striae on much of the surface of their chelae.

Genus *Pagurus* Fabricius, 1775

*Type species* — *Cancer bernhardus* Linné, 1758, by subsequent designation of Latreille (1810). Range: Early Cretaceous-Recent.

**Pagurus latidactylus** sp. nov.

Pl. 1, Figs 7-9; text-fig. 2c

*Derivation of name* — With reference to the width of the fixed finger.

*Material* — Holotype, a right propodus of a cheliped (EF-6.1 [M.91-100]); paratypes, left and right propodi (EF-6.2-9 [M.91-100]) and several fragments (EF-6.10-17 [M.91-100]).

*Description* — The only known parts are propodi of both chelipeds. Heterochely, if it existed, was probably moderate as left and right chelae are of the same size-range. The manus is almost rectangular with the upper and lower margins subparallel; the transverse section is subelliptical, deformed by flat zones on the upper sides. The upper margin is sharp, the lower one somewhat blunter. The fixed finger is extremely wide (Pl. 1, Fig. 9) and triangular in upper view with a row of rudimentary spines on the outer margin. Its tip is bent upwards. The surface of the chelae is ornamented with densely packed granules or flattened tubercles. One specimen (EF-6.3, Pl. 1, Fig. 7) of an internal mould, differs in having a narrow, pointed fixed finger; this may be due to sexual dimorphism, or the specimen may belong to another species.

*Discussion* — This species is quite unlike any other fossil pagurids in which the fixed finger is known by the flatness of that part. In the shape of the manus, *Pagurus marcei* of Via (1959) is probably the most similar fossil form to the Hungarian one. The tuberculation in *P. marcei* is much coarser and, unfortunately, Via's material consists only of specimens with broken fingers, thus precluding comparison in the most marked character.

Genus *Diogenes* Dana, 1853

*Type species* — *Pagurus miles* Fabricius, 1787, by subsequent designation of Stimpson (1859). Range: Miocene-Recent.

**Diogenes longimanus** sp. nov.

Pl. 1, Figs 10, 11; text-fig. 2d

*Derivation of name* — Alluding to the elongated propodus.

*Material* — Holotype, a left propodus of the cheliped (EGA-4.1 [M.91-101]) and paratype, a left propodus (EGA-4.2 [M.91-101]).

*Description* — The manus is flattened, slightly longer than high, its upper and lower margins are subparallel and keeled, the lower margin is decorated with a saw-like row of spines. Although lacking its tip, the fixed finger is long, its estimated length being almost as much as that of the manus. The manus is moderately convex in cross-section and the outer side is more convex than the inner side, the lower one third of which being almost flat, or even slightly concave in one specimen. The outer side is granulated around the base of the fixed finger and near the lower margin. On the inner side the granulation is confined to a narrow strip along the lower edge which bears a row of fine spines.

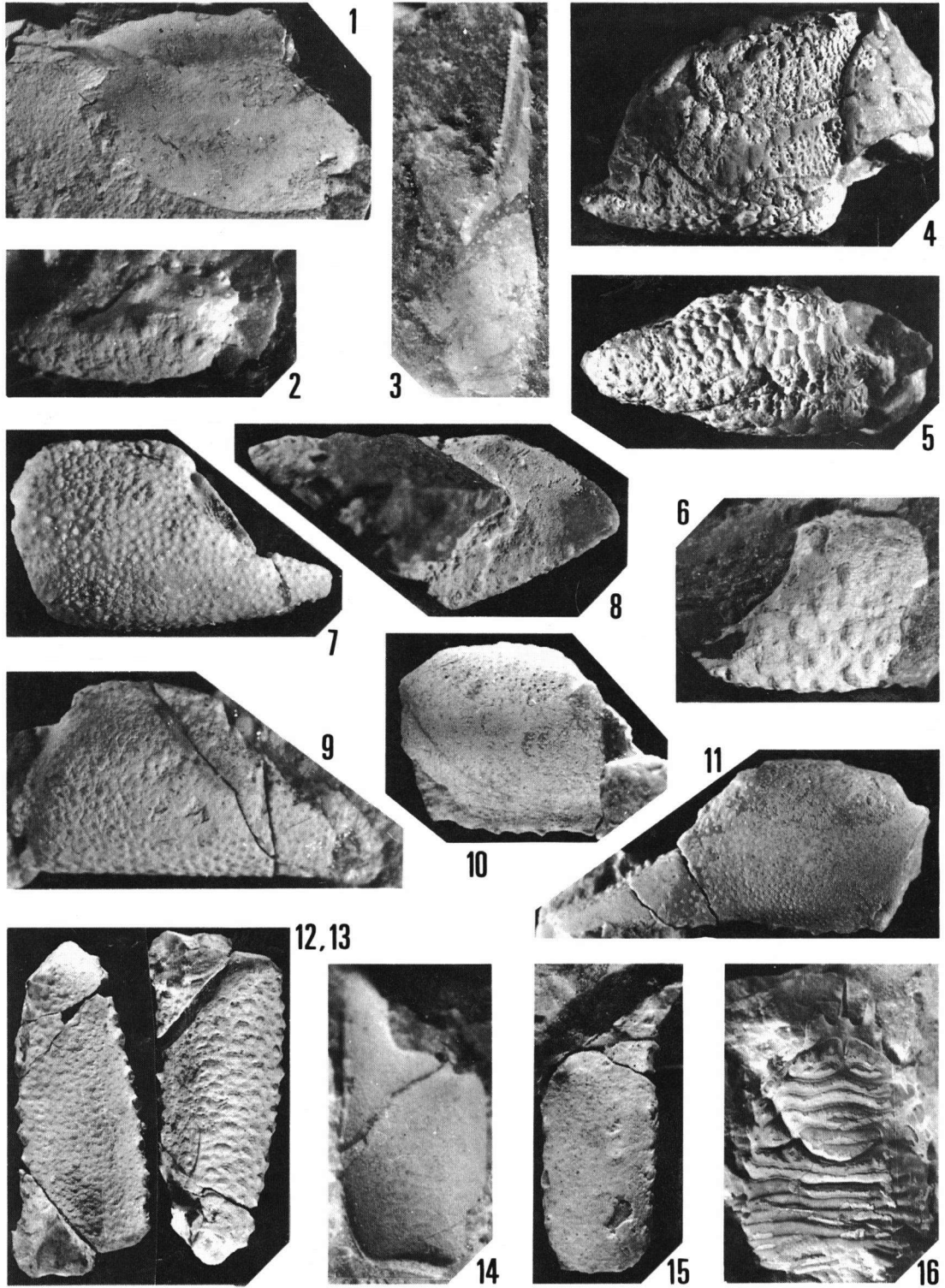
*Discussion* — The manus of this species is similar to that of *Diogenes matrensis* Müller, 1984 and *Diogenes extractatus* Stebbing, 1910, but the fixed finger is much longer in the present species.

Genus *Anapagurus* Henderson, 1886

PLATE 1

- Figs 1, 3 *Homarinae* ? sp., 1 - lateral view of carapace, EF-33.1 [M.91-97], x 7; 3 - outer surface of propodus, EF-33.4 [M.91-97], x 6.
- Fig. 2 *Paguristes oligotuberculatus* sp. nov., outer surface of left propodus, EF-8.1 [M.91-104], x 10.
- Figs 4-6 *Dardanus curtimanus* sp. nov., 4 - inner surface of left propodus, holotype, EK-6.1 [M.91-99], x 3; 5 - lower surface of propodus, EK-6.1 [M.91-99], x 3; 6 - outer surface of propodus, paratype, EF-5.1 [M.91-98], x 4.
- Fig. 7 *Pagurus* cf. *latidactylus* sp. nov., outer surface of internal mould of right propodus, EF-6.3 [M.91-100], x 5.6.
- Figs 8, 9 *Pagurus latidactylus* sp. nov., 8 - opposing margin of the fixed finger, EF-6.2 [M.91-100], x 5.6; 9 - outer surface of internal mould of right propodus, holotype, EF-6.1 [M.91-100], x 5.
- Figs 10, 11 *Diogenes longimanus* sp. nov., 10 - outer surface of left propodus, EGA-4.2 [M.91-101], x 4; 11 - inner surface of left propodus, holotype, EGA-4.1 [M.91-101], x 4.
- Figs 12, 13 *Galathea (Palaeomunida) defecta* (Lórenthey), 12 - inner surface of left propodus, EE-1.10 [M.91-114], x c. 3.5; 13 - outer surface of left propodus, EE-1.10 [M.91-114], x c. 3.5.
- Fig. 14 *Anapagurus* sp., inner surface of left propodus, EF-7.1 [M.91-102], x 10.8.
- Figs 15, 16 *Protomunida pentacantha* sp. nov., 15 - outer surface of right propodus, paratype EK-3.10 [M.91-115], x 4.2; 16 - dorsal view of holotype, EBM-1.1 [M.91-116], x 4.2.

PLATE 1



*Type species* — *Pagurus laevis* Bell, 1845, by subsequent designation of Holthuis (1962). Range: Miocene-Recent.

**Anapagurus** sp.

Pl. 1, Fig. 14; text-fig. 2f

*Material* — Left propodi of the cheliped (EF-7.1 [M.91-102], EBA-7.1 [M.91-103]).

*Description* — The propodus is elongate with the manus highest in its distal part and moderately convex in cross-section. It is almost straight longitudinally and smooth apart from a faint ridge running along the lower margin towards the tip of the fixed finger, which is obscured by matrix.

*Remarks* — The outline of the propodi strongly suggests that they belong to a pagurid. The tubercles situated on the proximal part of the manus on the Miocene species, *Anapagurus miocenicus* Müller, 1979 and *Anapagurus marginatus* Müller, 1979, are wanting in the present specimens, although the ridge along the lower edge is similar to that on *A. marginatus*. A characteristic of the genus is a marked heterochely with the right cheliped invariably the larger and the previously remarked Miocene species follow this trait. The present specimens, however, are from the left-hand side and — presenting only the outer side — do not allow sufficient comparison; therefore we prefer not to give them specific status for the time being.

Genus *Paguristes* Dana, 1853

*Type species* — *Paguristes hirtus* Dana, 1853, by subsequent designation of Stimpson (1859). Range: Cretaceous-Recent.

**Paguristes oligotuberculatus** sp. nov.

Pl. 1, Fig. 2; text-fig. 2e

*Derivation of name* — Alluding to the low number of tubercles on the manus.

*Material* — A left propodus of the cheliped (EF-8.1 [M.91-104]).

*Description* — The small cheliped is elongate with the lower and short upper margins curved. Four strong tubercles line the upper margin and there is the basal scar of a tubercle beneath the second one; another line of tubercles is situated on the outer side of the manus below the midline. The fixed finger is wide, probably spoon-shaped, but its cutting surface is obscured.

*Discussion* — This species shows some similarities to the Badenian (Middle Miocene) *Paguristes cserhatensis* Müller, 1984 and to some extant forms such as *Paguristes rosaceus* Barnard, 1947, but is longer in relation to width and the number of rows of tubercles is reduced.

Paguridae sp. indet.

*Material* — Fragments of carapaces (EF-34.1-4 [M.91-105]).

*Description* — The elongate, thick shield-like fragments probably represent median anterior parts of carapaces of uncertain affinities. Their outer surface is smooth, while the inner one shows a complicated system of grooves and short striae which may partly represent muscle insertions. A U-shaped groove which divides the 'shield' into two subequal parts may correspond to the cervical furrow; behind it are two obliquely placed grooves on the inner side.

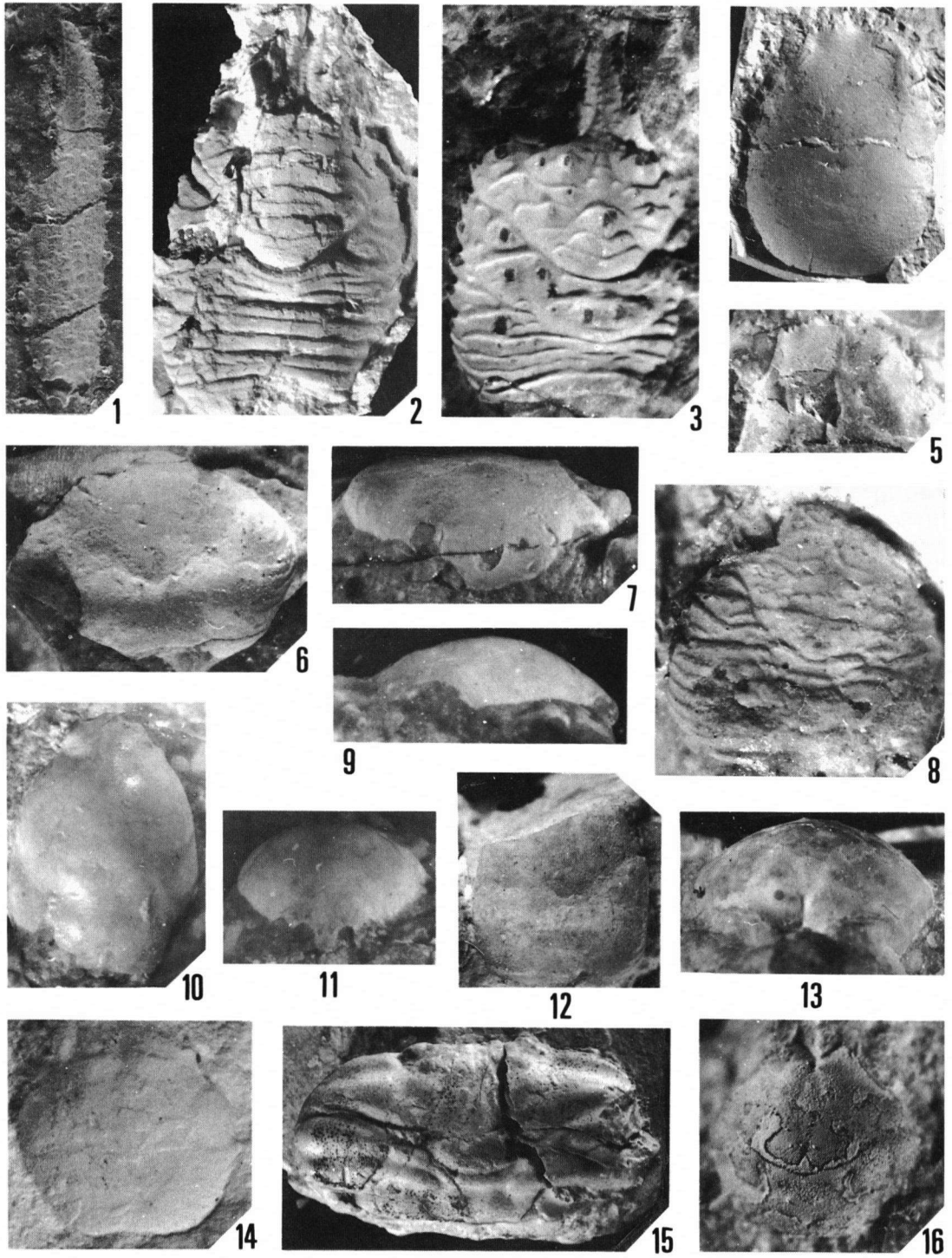
*Remarks* — The specimens show some remote simi-

PLATE 2

- Figs 1, 2 *Galathea (Palaeomunida) defecta* (Lôrenthey), 1 - inner surface of left propodus, EK-2.1 [M.91-122], x 3.6; 2 - dorsal view of carapace, latex from external mould of EE-1.1 [M.91-114], x 3.
- Fig. 3 *Galathea (Acanthogalathea) parva* subgen. et sp. nov., dorsal view of carapace, holotype, EF-3.1 [M.91-106], x 11.
- Figs 4, 5 *Longoporcellana denticulata* gen. et sp. nov., 4 - dorsal view of carapace, latex from external mould of holotype, EF-1.1 [M.91-120], x 8; 5 - anterior dorsal view showing denticulated frontal margin, EF-1.1 [M.91-120], x 8.
- Figs 6, 7 *Polyonyx arcuatus* sp. nov., 6 - dorsal view of carapace, holotype EK-2.1 [M.91-122], x 8.7; 7 - frontal view of carapace, EK-2.1 [M.91-122].
- Fig. 8 *Petrolisthes ? striatissimus* sp. nov., dorsal view of carapace, holotype, EGA-5.1 [M.91-123], x 10.9.
- Figs 9-11 *Ovocarcinus elongatus* gen. et sp. nov., 9 - lateral view of carapace, holotype, EF-35.1 [M.91-126], x 10; 10 - dorsal view of carapace, EF-35.1 [M.91-126], x 10; 11 - lateral view of carapace, EF-35.1 [M.91-126], x 10.
- Fig. 12 Porcellanidae sp. B, dorsal view of carapace, EGF-3.1 [M.91-125], x 7.8.
- Figs 13, 16 *Dromilites fossata* sp. nov., 13 - frontal view of carapace, holotype, EGF-5.1 [M.91-131], x 7.5; 16 - dorsal view of carapace, EGF-5.1 [M.91-131], x 6.4.
- Fig. 14 Porcellanidae sp. A, dorsal view of carapace, latex from external mould of EK-5.1 [M.91-124], x c. 17.
- Fig. 15 *Gemellarocarcinus loerentheyi* Checchia-Rispoli, dorsal view of carapace, EK-9.1 [M.91-141], x 2.4.



PLATE 2



larities to pagurid carapaces, but it is difficult to find the analogous structures. Extant pagurid carapaces are generally much shorter and wider.

Superfamily Galattheoidea Samouelle, 1819  
Family Galatheididae Samouelle, 1819  
Genus *Galathea* Fabricius, 1793  
Subgenus *Acanthogalathea* subgen. nov.

*Type species* — *Galathea (Acanthogalathea) parva* sp. nov.

*Diagnosis* — *Galathea*-like carapace, striation typical for *Galathea*, strong spines on branchial, cardiac, mesogastric and protogastric regions respectively.

***Galathea (Acanthogalathea) parva* sp. nov.**

Pl. 2, Fig. 3; text-fig. 2h

*Derivation of name* — From the Latin, small.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-3.1 [M.91-106]).

*Description* — The carapace is quadrate, without the rostrum it is about as long as wide. The dorsal surface is strongly sculptured. The cervical furrow is deep and a postcervical one is also developed laterally. Meta- and mesogastric lobes are well delimited. There are three strong spines on the epibranchial lobe, one on the mesobranchial lobe and two on the cardiac region. These spines are broken, but their length can well be estimated to have been 0.2-0.5 mm. On the mesogastric lobe there is also a spine which was probably the longest. The spines on the protogastric and hepatic regions are smaller. The dorsal ridges are arranged in a *Galathea*-like manner, the hinder ones are longer, those situated on the anterior parts are curved and, except posteriorly, most of the dorsal ridges are produced into strong spines at the lateral margins. The rostrum, slightly V-shaped in cross-section, is long and slender and has two spines near its base; on the proximal half of the median line is a ridge composed of tubercles. The rostral tip is obscured, so its full length can only be estimated as about half the carapace length.

*Discussion* — Although the form and striation of the carapace is typical for *Galathea* species — e.g. *Galathea strigosa* (Linné, 1761) and *Galathea vanstraeleni* Bachmayer, 1950 — the strong dorsal spines and narrow rostrum with subbasal spines argue for separation at subgeneric level.

Subgenus *Palaeomunida* Lörenthey, 1901

*Type species* — *Palaeomunida defecta* Lörenthey, 1901, by monotypy. Range: Middle-Late Eocene.

*Remarks* — Separation of *Palaeomunida* from *Galathea* on generic level seems not to be well established. The form and striation of the carapace, as well as that of the chelae are typical for *Galathea*, also the shape of the rostrum of *Palaeomunida*, regarded as diagnostic for the genus (Glaessner, 1969) is similar to some fossil and extant species of *Galathea*. The median ridge on the rostrum, consisting of granules, is to some extent present in *G. strigosa* and in the related *G. vanstraeleni*. The size and form of the lateral spines and the rostrum does not differ substantially in the above mentioned three species. Contrarily, however, in the extant species there is a marked variation in the form of the rostrum from the spinose *G. strigosa* type to the almost entire *Galathea intermedia* Lilljeborg, 1851 type. Despite this close similarity, it is considered prudent to retain *Palaeomunida*.

***Galathea (Palaeomunida) defecta***

(Lörenthey, 1901)

Pl. 1, Figs 12, 13; Pl. 2, Figs 1, 2; text-fig. 2g

- 1901a *Palaeomunida defecta* Lörenthey, p. 807, pl. 1, fig.  
1969 *Palaeomunida defecta* Lörenthey — Via, p. 405 (with synonymy).  
1975 *Galathea* sp. — Müller, pp. 516, 520.

*Material* — The holotype is deposited in Magyar Állami Földtani Intézet. Eight carapaces, 1 propodus (EF-4.1-9 [M.91-107]); 21 carapaces, 7 propodi, 3 sternal plates (EK-4.1-31 [M.91-108]); 3 carapaces (EGA-3.1-3 [M.91-112]); 24 carapaces, 5 propodi, 1 sternal plate (EGF-2.1-30 [M.91-113]); 2 carapaces, 1 propodus (EBM-2.1-3 [M.91-110]); 7 carapaces, 1 propodus (EBV-1.1-8 [M.91-111]); 1 propodus (EK-2.1 [M.91-122]); 9 carapaces, 6 propodi (EE-1.1-15 [M.91-114]); 3 carapaces J.S.H. Collins Collection.

*Remarks* — Lörenthey gave a detailed description (in Lörenthey & Beurlen, 1929). Our figures provide a more detailed view of the rostrum on which there are a pair of basal (intraorbital) spines, two pairs of lateral spines and a spinose tip. It appears that Lörenthey added an extra spine to his figure without justification. The species has also been reported from Sicily (di Salvo, 1933).

Genus *Protomunida* Beurlen, 1930

*Type species* — *Galathea munidoides* Segerberg, 1900, by original designation. Range: Palaeocene-Late Eocene.

**Protomunida pentacantha** sp. nov.

Pl. 1, Figs 15, 16; text-fig. 2i

*Derivation of name* — Alluding to the five rostral spines.

*Diagnosis* — A *Protomunida* with a flat rostral base and five rostral spines.

*Material* — Holotype, a carapace (EBM-1.1 [M.91-116]); paratypes, 1 carapace, 12 propodi, ?1 sternal plate (EK-3.1-28 [M.91-115]); 4 carapaces, six propodi, 1 sternal plate (EGA-2.1-11 [M.91-118]); 4 carapaces (EGF-1.1-4 [M.91-119]); 5 carapaces (EBM-1.2-5 [M.91-116]); 3 carapaces, 5 propodi (EBV-2.1-8 [M.91-117]).

*Description* — The carapace without rostrum is about one fourth longer than wide. Only the anterior part of the mesogastric lobe is delimited. The cervical furrow is conspicuous, while other furrows are obscured by strong striation which is quite even; there are 7-10 striae behind the cervical furrow and 7 or 8 before it. On the epibranchial lobe the striae are replaced by 6 or 7 tubercles. Across the postfrontal part is a row of 6 spiniform tubercles. The base of the rostrum is flat, wide and decorated with small scale-like tubercles; it gives rise to five rostral spines the median one of which is separated from its neighbours by a space wider than itself, while the outer ones are situated in close pairs. None of these spines is preserved in its original length, but the median one probably reached one third of the carapace length without rostrum.

Small chelae are found in most localities where the carapaces of *Protomunida* are abundant. These are typical for galatheids and their size matches the carapaces of *Protomunida*; without doubt, they belong to the present species. The manus is about twice as long as high, the upper and lower margins each bear 4 or 5 spines. There is a row of 4 or 5 tubercles at about the lower third of the outer surface which is covered with faint scale-like tubercles which tend to fuse into inconspicuous ridges. The sternal plate is insufficiently preserved to allow adequate description.

*Discussion* — The peculiar *Munida*-like rostrum with the *Galathea*-like carapace closely allies *Protomunida pentacantha* to the Early Palaeocene (Danian) *Protomunida primaeva* (Segerberg, 1900), in which there are only three rostral spines, but the sculpture is much the same in the two species. *Protomunida pentacantha* seems to be closest to *Sadayoshia acroporae*

Baba, 1972; the arrangement of the rostral spines, the presence of a flat surface at the base of the rostrum, the spinose postfrontal ridge as well as tubercles on the epibranchial lobe relates the two species. On Baba's (1972) species the postfrontal ridge is almost straight, but widely A-shaped in *P. pentacantha*.

Family Porcellanidae Haworth, 1825

*Remarks* — Without doubt, it is because of the small size of most porcellanid species that their fossil record is extremely poor. Apart from some recently recognised Miocene species (Georgiades-Dikeoulia & Müller, 1984; Müller, 1984a, b) only one Cretaceous species, *Porcellana antiqua* Milne Edwards, 1882 and some doubtful species based on limb fragments (Rathbun, 1945) have been described.

Genus *Longoporcellana* gen. nov.

*Type species* — *Longoporcellana denticulata* sp. nov.

*Derivation of name* — With reference to the carapace outline, which is unusual for the family, and the established generic name *Porcellana*.

*Diagnosis* — An elongated, flat carapace, broadest in its hinder part, with a wide, short triangular rostrum.

**Longoporcellana denticulata** sp. nov.

Pl. 2, Figs 4, 5; text-fig. 2j

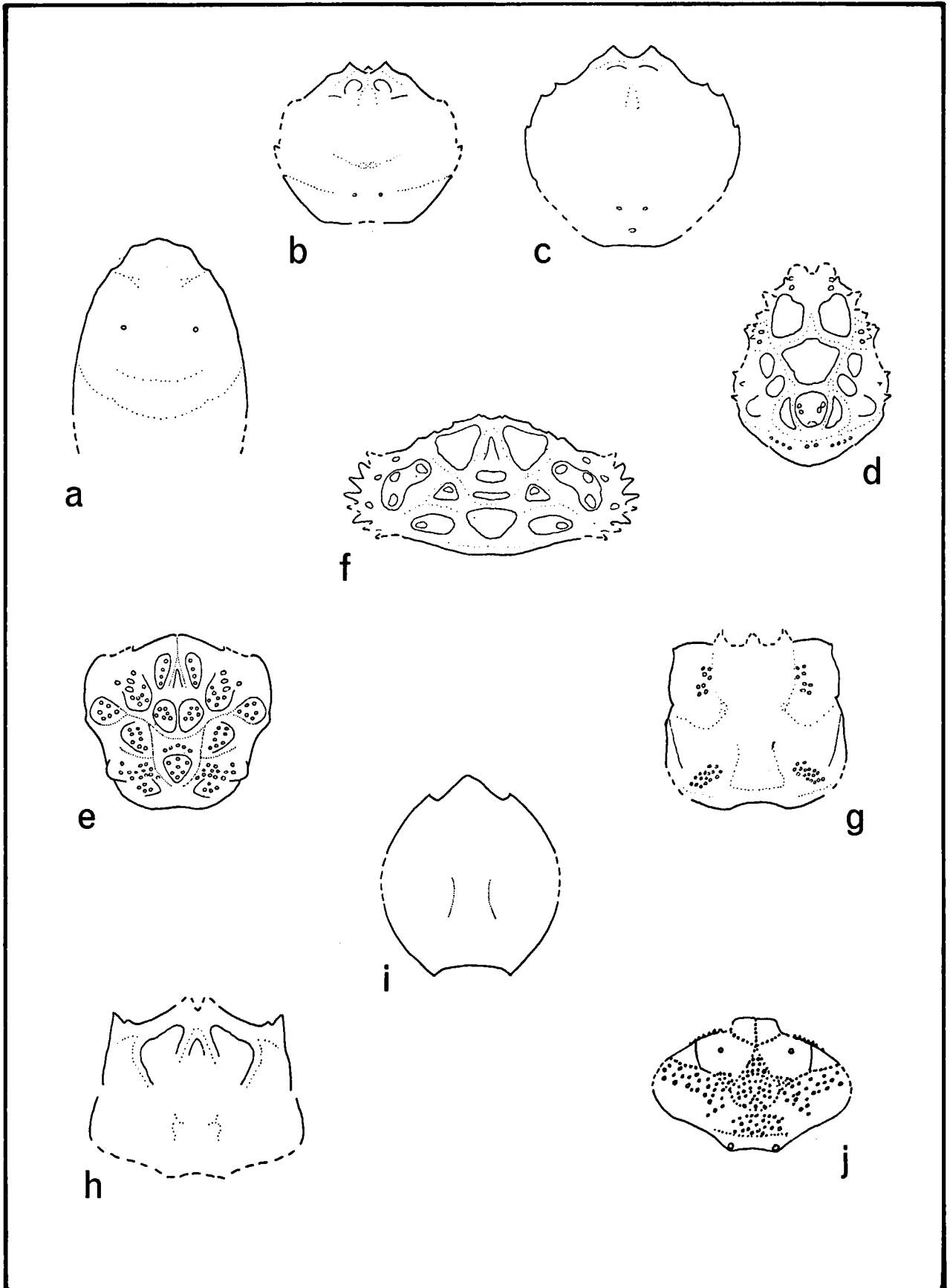
*Derivation of name* — After the denticulated rostrum.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-1.1 [M.91-120]), and paratypes (?EF-1.2 [M.91-120], EBK-2.1 [M.91-121]).

*Description* — The carapace is ovoid or pyriform in outline, about one third longer than broad, flat anteriorly and moderately convex about the branchial parts. A rudimentary cervical furrow is situated slightly behind mid-carapace length. The orbital margins are slightly elevated above the surface of the carapace in a sublateral position. The wide, triangular rostrum is ornamented with 8 or 9 denticles on each side, its tip is obscured; lateral teeth or spines are probably absent, but the margins are partly covered with matrix. There are faint, fine transverse striae on the rostrum, between the orbits and towards the posterolateral margin.

*Discussion* — The position of the orbitofrontal margin and the entire carapace strongly suggests



porcellanid affinity although most porcellanids are much less elongated. The species and thus the genus is superficially similar to extant American *Minyocerus* spp., but the shape of the rostrum, position of the orbital margins and general outline of the carapace are markedly different. One specimen (EF-1.2) differs in being wider and having a pair of postfrontal ridges; it may possibly represent another, related species.

Genus *Polyonyx* Stimpson, 1859

*Type species* — *Porcellana macrocheles* Stimpson, 1859 (= *gibbesi* nom. nov. Haig, 1956) by original designation. See Haig (1956, pp. 28, 29) for explanation of homonymy. Range: Late Eocene-Recent.

***Polyonyx arcuatus* sp. nov.**

Pl. 2, Figs 6, 7; text-fig. 2k

*Derivation of name* — Alluding to the inflated, almost globular form of the carapace.

*Diagnosis* — Carapace wider than long with a wide, deflected rostrum and inflated branchial regions.

*Material* — Holotype, a carapace (EK-2.1 [M.91-122]).

*Description* — The width of the carapace is about four fifths of the length; it is strongly arched longitudinally, laterally less convex in its median part, but strongly inflated about the branchial regions. In dorsal view the carapace is nearly elliptical and the wide, strongly deflected rostrum is prominent; it is rounded-triangular in outline, smooth with an undulating margin along which runs a faint ridge. The orbital sinus is shallow. The V-shaped cervical furrow is only visible in tangential illumination. On the lateral margins of the branchial regions are 7 or 8 step-like ridges reaching to about one sixth of the carapace width, transverse at their inner ends and directed forwards laterally. The rest of the carapace surface is smooth.

*Discussion* — The carapace agrees by and large with that of Recent members of the genus, and in having a rounded outline to the branchial regions it is similar to *Pachycheles* spp. While its outline is close to

*Polyonyx obesulus* of Miers [1884] (which lacks all but one of the branchial ridges) the marked grade of deflection of the front is uncommon for extant *Polyonyx* spp., or any other extant porcellanids. Although the shape of the cervical furrow slightly resembles that of some dynomenids, the absence of a sharp anterolateral margin and completely different orbitofrontal margin eschews the possibility of a dynomenid or brachyuran affinity. The faint ridges on the branchial regions, although of inferior taxonomic value, also suggest a porcellanid relationship.

Genus *Petrolisthes* Stimpson, 1859

*Type species* — *Porcellana violacea* Guérin-Méneville in Duperry, 1831, by monotypy. Range: ?Late Eocene-Recent.

***Petrolisthes ? striatissimus* sp. nov.**

Pl. 2, Fig. 8; text-fig. 2l

*Derivation of name* — With reference to the uncommonly striated carapace.

*Diagnosis* — Carapace almost flat and strongly striated.

*Material* — Holotype, a carapace (EGA-5.1 [M.91-123]).

*Description* — The carapace subquadrate with rounded angles, almost as long as wide without the rostrum, of which only the basal part is preserved. The dorsal surface is flat except near the lateral margins where it is somewhat convex. The lateral margins converge slightly anteriorly; they were probably neither spinose nor denticulated. The posterior margin is slightly concave. The cervical furrow is deep; a pair of shallower furrows delimit the anterior part of the mesogastric lobe from the proto-gastric lobe. Other furrows are obscured by the conspicuous striation. Only the left orbital sinus is preserved; it is deep and delimited laterally by a sharp protruding spine. The transverse ridges are very strong, the most conspicuous being situated on the branchial regions. Those on the meso- and metabranchial lobes are subparallel while those on the epibranchial are more complicated.

*Discussion* — The nature of the carapace is typical for many extant porcellanids, but it bears a system of ridges uncommonly strong for the family and more comparable to that of *Galathea* species. This feature differentiates it from other known fossil representatives of the family. The carapace outline of *P. ? striatissimus* is similar to that of the Miocene

Fig. 3. Diagrammatic views of: a - *Ovocarcinus elongatus* gen. et sp. nov., b - *Dromilites fossata* sp. nov., c - *Dromilites subglobosa* sp. nov., d - *Nanomaja simplex* gen. et sp. nov., e - *Kromtitis pentagonalis* sp. nov., f - *Mesolambrus declinatus* gen. et sp. nov., g - *Cynomomus primitivus* sp. nov., h - *Ethusa evae* sp. nov., i - *Ovamene franciae* gen. et sp. nov., j - *Gemmacarcinus fossatus* gen. et sp. nov.

*Pisidia kokayi* (Müller, 1974), but, again, the striation readily distinguishes them.

Porcellanidae sp. A  
Pl. 2, Fig. 14; text-fig. 2m

*Material* — Two carapaces (EK-5.1-2 [M.91-124]).

*Description* — The small carapace is almost circular in outline with a prominent wide, flat rostrum. Two wide postfrontal ridges are separated by a wide longitudinal furrow. The cervical furrow is only visible near the lateral margins. The orbital margins are obliquely placed. A faint striation is visible on the marginal part of the branchial regions.

*Discussion* — Because of the poor state of the preservation it seems unwise to give a formal taxonomic status to the specimens, one of which is a very small external mould and the other is but fragmentary. It can be stated, however, that the species is unlike any described fossil form, but more closely resembles the extant Atlantic and Mediterranean *Porcellana platycheles* (Pennant, 1777).

Porcellanidae sp. B  
Pl. 2, Fig. 12; text-fig. 2n

*Material* — A decorticated carapace lacking frontal parts (EGF-3.1 [M.91-125]).

*Description* — The carapace is subquadrate with almost straight lateral margins. Remains of five or six marginal spines terminate five or six of the striae faintly visible on the branchial region. The cervical furrow is deep and V-shaped.

*Discussion* — As in the case of Porcellanidae sp. A, the carapace is unlike any known fossil form, but its incomplete preservation precludes formal classification.

Family *incertae sedis*  
Genus *Ovocarcinus* gen. nov.

*Derivation of name* — Alluding to the egg-shaped carapace.

*Type species* — *Ovocarcinus elongatus* sp. nov.

*Diagnosis* — A transversely very convex egg-shaped carapace with a strongly deflected semicircular front and a small orbital sinus.

***Ovocarcinus elongatus* sp. nov.**  
Pl. 2, Figs 9-11; text-fig. 3a

*Derivation of name* — With reference to the elongated carapace.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-35.1 [M.91-126]).

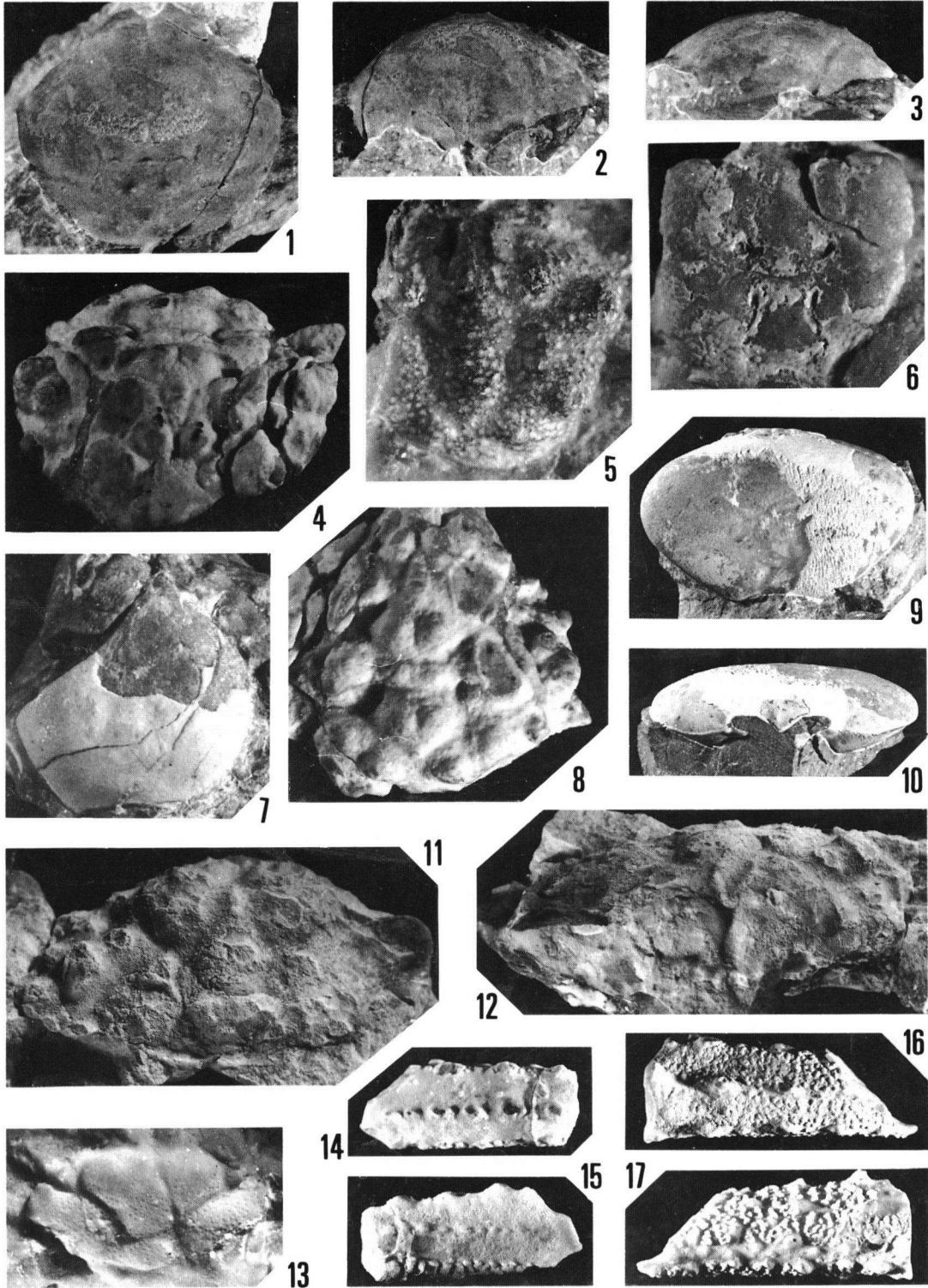
*Description* — Only the anterior part of the carapace, possibly three fourths of the whole, is preserved. It is elongate egg-shaped in outline, almost semicircular in transverse section. The surface is smooth with slight undulations. On the postfrontal part are two wide, shallow depressions on either side of the midline. The cervical furrow is broadly V-shaped where it crosses the midline near the middle (as preserved) of the carapace; behind the furrow is a wide conspicuous depression which may represent the postcervical furrow. Behind that is a short, median furrow. The orbitofrontal margin is narrow and the orbital sinus semicircular; the rostrum-like frontal feature is very narrow, subvertical with entire margins, slightly convergent distally. There is another embayment behind the orbital sinus, the two forming a figure 3. The regions are poorly defined.

*Discussion* — The carapace is highly unusual in its

PLATE 3

- Figs 1-3 *Dromilites subglobosa* sp. nov., 1 - dorsal view of carapace, holotype, EF-9.1 [M.91-127], x 3.5; 2 - frontal view of carapace, EF-9.1 [M.91-127], x 3.5, 3 - left lateral view of carapace, EF-9.1 [M.91-127], x c. 3.4.
- Figs 4, 5, 8 *Kromtitis pentagonalis* sp. nov., 4 - frontal view of carapace, holotype, EBA-4.1 [M.91-133], x 4; 5 - inner view of external mould showing fine surface granulation, paratype EGA-6.1 [M.91-134], x 7.2; 8 - dorsal view of carapace, EBA-4.1 [M.91-133], x 4.5.
- Fig. 6 *Cymonomus primitivus* sp. nov., dorsal view of carapace, holotype, EK-10.1 [M.91-135], x 8.
- Fig. 7 *Ovamene francae* gen. et sp. nov., dorsal view of carapace, holotype, EF-12.1 [M.91-143], x 6.3.
- Figs 9, 10 *Cyamocarcinus angustifrons* Bittner, 9 - dorsal view of carapace, EF-11.6 [M.91-136], x 1; 10 - frontal view of carapace, EF-11.1 [M.91-136], x 1.6.
- Figs 11, 12 *Mesolambrus declinatus* gen. et sp. nov., 11 - dorsal view of internal mould carapace, holotype, EGA-9.1 [M.91-151], x 2.4; 12 - frontal view of internal mould of carapace, EGA-9.1 [M.91-151], x 2.4.
- Fig. 13 *Gemmocarcinus fossatus* gen. et sp. nov., dorsal view of carapace, holotype, EBA-8.1 [M.91-145], x 8.4.
- Figs 14-17 ? *Mesolambrus declinatus* gen. et sp. nov., 14, 15 - inner and outer surfaces of propodus, EK-11.1, x 4; 16, 17 - inner and outer surfaces of propodus, EK-11.2, x 4.

PLATE 3



form. It may superficially resemble some Hippidae and, to some extent, some Dromiidae (e.g. *Noetlingia* Beurlen, 1928). The orbitofrontal margin is quite unlike that of a dromiid, also the lateral limits of the carapace seem to correspond to lineae anomuricae rather than to the lateral margins of a dromiid. Consequently, we prefer to place the species in a new genus of uncertain, possibly 'anomuran' affinities.

Infraorder	Brachyura Latreille, 1803
Section	Dromiacea de Haan, 1833
Superfamily	Dromioidea de Haan, 1833
Family	Dromiidae de Haan, 1833
Genus	<i>Dromilites</i> H. Milne Edwards, 1837

*Type species* — *Dromia bucklandii* H. Milne Edwards, 1837, by monotypy. Range: Early Eocene-Miocene.

***Dromilites fossata* sp. nov.**

Pl. 2, Figs 13, 16; text-fig. 3b

*Derivation of name* — Alluding to the deep cervical and branchiocardiac furrows.

*Diagnosis* — Carapace subpentagonal in outline with granular lateral spines; a small cardiac region intrudes upon base of the urogastric lobe.

*Material* — Holotype, a carapace (EGF-5.1 [M.91-131]) and paratype, a carapace (EK-13.1 [M.91-130]).

*Description* — The carapace is subpentagonal in outline, about as long as wide, widest about midlength. Viewed from the side the mid-gastric region forms the highest part, there is a shallow urogastric depression and the downward curve of the front is steeper than that to the posterior margin. It is rather boldly arched in transverse section. The anterolateral margins are thin with, possibly, four spines of which the first, just behind the orbit, and the fourth are the longest. The subparallel lateral margins are granulate rather than spinose. Short, posterolateral margins lead by way of sharp posterior angles to a narrow, slightly convex posterior margin bounded by a shallow groove. The (partly obscured) orbitofrontal margin occupies about four fifths of the greatest carapace width; the slightly produced front flattens a little from the general curvature and its margins are raised and continuous with the oblique upper orbital margins. The orbits are narrowly ovate. The cervical furrow is distinct and broadly V-shaped medially; directed a little forward from the lateral angles of the mesogastric lobe it

weakens as it curves outwards to a shallow notch at the lateral margin. Thin branchiocardiac furrows running to the margin from the cardiac region are accentuated by a posterior depression in the epibranchial lobes which also produces a peninsular effect to small, triangular mesogastric lobes. A tumid portion of the protogastric lobe rises just behind small round epigastric lobes set close to the midline and encloses the tip of the anterior mesogastric process; the lobe itself is poorly defined and divided posteriorly by a median furrow. The almost heart-shaped cardiac region has three tubercles set in an inverted triangle and there is a distinct pit between the anterior pair which intrude upon the base of the urogastric lobe giving it the appearance of two triangles; the sides of the lobe are entrenched by the epimeral muscle scars.

*Discussion* — The absence of lateral spines immediately distinguishes *Dromilites corvini* (Bittner, 1893) from *D. fossata*, which has rather more in common with *Dromilites pastoris* Via, 1965 from the Middle Lutetian of Spain. A second Spanish species, *Dromilites vicensis* Corinas, 1973, from the Biarritzian (Middle Eocene) is more lobate and lacks the cardiac tubercles. *Dromilites americana* Rathbun, 1935, from the Palaeocene of the U.S.A., has a prominent branchiocardiac furrow and a relatively weaker cervical furrow, while *Dromilites simplex* Quayle & Collins, 1981 from the Ypresian and Middle Auversian of England has thin, somewhat flared anterolateral margins and, apart from a large cardiac region, poorly defined regions.

***Dromilites subglobosa* sp. nov.**

Pl. 3, Figs 1-3; text-fig. 3c

*Derivation of name* — With reference to the longitudinal section.

*Material* — Holotype, a carapace (EF-9.1 [M.91-127]) and paratypes (EF-9.2-10 [M.91-127], EK-7.1-4 [M.91-128], EBM-3.1 [M.91-129]).

*Diagnosis* — Carapace almost circular in outline with a weak posterior constriction coincident with dorsal troughs; furrows weakly developed.

*Description* — The carapace is small, almost circular in outline with the trace of a constriction posteriorly. In transverse section it is strongly arched anteriorly, but excavations coincident with the constriction in outline begin close to the midline and rapidly deepen and broaden towards the margins; longitudinally it curves steeply from just behind the front to about midlength and becomes flatter to the



posterior margin. The front is deeply divided by a U-shaped notch leading back in a median groove which divides behind a pair of round tumid epigastric lobes to embrace the tip of the anterior mesogastric process. Thin, slightly raised upper orbital margins diverge from the midline at an angle of about 50° and terminates in a small spine. A spine, elongated posteriorly, takes up all the anterolateral margin and a short notch, representing the lateral part of the cervical furrow, separates it from a similar spine on the lateral (epibranchial) margin; there is an obscure spine behind the branchiocardiac notch. The median part of the cervical furrow is a faint, almost straight depression in which a pair of gastric pits are set apart about the same distance as the frontal notch. Excavations on the dorsal surface coincident with the constriction in outline begin close to the midline and rapidly deepen and broaden towards the margin.

*Discussion* — The weakly developed cervical furrow and absence of a branchiocardiac furrow, together with the dorsal troughs at once distinguishes *D. subglobosa* from *D. fossata*.

Genus *Kromtitis* Müller, 1984a (*non* Papp *et al.*, 1978=*nomen nudum*)

*Type species* — *Dromilites koberi* Bachmayer & Tollmann, 1953, by original designation. Range: Eocene-Miocene.

***Kromtitis pentagonalis* sp. nov.**

Pl. 3, Figs 4, 5, 8; text-fig. 3e

*Derivation of name* — From the carapace outline.

*Diagnosis* — Carapace pentagonal in outline, the regions are well defined and nodose.

*Material* — Holotype, a carapace (EBA-4.1 [M.91-133]) and paratypes (EF-10.1-3 [M.91-132], EGA-6.1 [M.91-134], EBA-4.2-4 [M.91-133]).

*Description* — The carapace is pentagonal in outline, medially flattened with steep sides in transverse section and almost flat longitudinally. The broad orbital margin forms an angle of about 30° and the raised edges of the pointed, steeply downturned front lead directly to the upper orbital margins with a fine groove behind. The narrowly ovate orbits are set close together. A median sulcus behind the front divides at the tip of a short, triangular anterior mesogastric process which extends midway between narrow, elongate protogastric lobes. The urogastric lobe is depressed and has a pair of low granules. It is

deeply embayed round the base of the mesogastric lobe which is divided medially by a groove. Crossing the midline a little posterior to carapace midlength, the cervical furrow curves narrowly round the base of the mesogastric lobe before passing forward and outward in two loops round the meso- and epibranchial lobes. In young individuals these lobes are each divided into two nodes. The cardiac region is attenuated posteriorly and separates the basal part of deeply divided metabranchial lobes. The sculpture becomes more pronounced with age and the entire dorsal surface is covered with numerous small granules of more or less even size as can be seen on an external mould (Pl. 3, Fig. 5).

*Discussion* — The Miocene species *Kromtitis koberi* is more circular in outline, the epi- and mesobranchial lobes are more noticeably divided in larger specimens and there are five, rather than two nodes on the cardiac region.

Family Cymonomidae Bouvier, 1898  
Genus *Cymonomus* A. Milne Edwards, 1880  
[*Cymonomus* ICZN Opinion 712, 1964, p. 337]

*Type species* — *Cymonomus quadratus* A. Milne Edwards, 1880, by monotypy. Name 1618 on Official List. Range: Late Eocene-Recent.

***Cymonomus primitivus* sp. nov.**

Pl. 3, Fig. 6; text-fig. 3g

*Derivation of name* — Indicating an early form of the genus.

*Diagnosis* — Carapace subquadrate, the protogastric lobes reach the frontal margin at the outer orbital angles and there is a granule on the anterior angles.

*Material* — A decorticated carapace, holotype (EK-10.1 [M.91-135]).

*Description* — The carapace is subquadrate in outline, almost flat in longitudinal and transverse sections. Parallel lateral margins lead by narrowly rounded posterior angles to a slightly concave posterior margin bounded by a thin ridge. The anterolateral margins are abruptly rounded and have a small granule. A vestige of the outer orbital angle indicates a slightly protruding orbitofrontal margin. Anteriorly the edges are rounded and the sides are inclined under at about 45°; the branchial sides are a little splayed out. The protogastric furrow reaches the front alongside the outer orbital angle. The cervical furrow is interrupted at the midline by

an extension of a narrow, slightly crescentic urogastric lobe, it turns sharply up to pits at the basal angles of the mesogastric lobe, unites with the protogastric furrow then loops sharply back and outwards to the margin a little forward of mid-carapace length. Branchiocardiac furrows run parallel to the lateral parts of the cervical furrow. The mesogastric lobe is pentagonal and its short anterior process does not reach the front. Deep pits flank the pentagonal cardiac region which has three granules in an inverted triangle. A depressed, elongate tubercle on the hepatic region adjoins the protogastric furrow. Minute granules are to be seen on the remaining shell-surface.

*Discussion* — The subquadrate carapace, narrow orbitofrontal margin and disposition of the grooves and lobes conform remarkably well with some Recent members of the genus. Where the furrows appear much deeper in *C. primitivus* the (missing) shell-thickness would in all probability have softened their apparent harshness in the present specimen. The protogastric furrows are subdued in *Cyonomus quadratus andamanicus* Alcock, 1905, but their course can be projected to the outer orbital angles, the cervical furrow is similarly interrupted at the midline. The most prominent marginal spine on the Recent *Cyonomus granulatus* (Thompson, 1873) and the only spine on *Cyonomus normani* Lanchester, 1903 occurs at the angle of the anterolateral margins similar to *C. primitivus*. Granules on preserved parts of the shell near the posterior margin are similar to those on *C. granulatus* and *C. normani*.

Family     Dynomenidae Ortmann, 1892  
Genus       *Cyamocarcinus* Bittner, 1883

*Type species* — *Cyamocarcinus angustifrons* Bittner, 1883, by monotypy. Range: Late Eocene.

**Cyamocarcinus angustifrons** Bittner, 1883  
Pl. 3, Figs 9, 10

- 1883 *Cyamocarcinus angustifrons* Bittner, p. 310, pl. 1, fig. 8.
- 1897 *Cyamocarcinus angustifrons* Bittner — Lörenthey, p. 155.
- 1969 *Cyamocarcinus angustifrons* Bittner — Via, p. 372.
- 1975 *Cyamocarcinus angustifrons* Bittner — Müller, pp. 516, 520.

*New material* — Carapaces EGA-7.1 [M.91-140], EF-11.1-9 [M.91-136], EK-8.1-3 [M.91-137], EBA-6.1-6 [M.91-138], EBK-4.1 [M.91-139].

*Remarks* — Nothing further can be added to the original description.

Genus     *Gemmellarocarcinus* Checchia-Rispoli, 1905

*Type species* — *Gemmellarocarcinus loerentheyi* Checchia-Rispoli, 1905, by monotypy. Range: Middle-Late Eocene.

**Gemmellarocarcinus loerentheyi**  
Checchia-Rispoli, 1905  
Pl. 2, Fig. 15

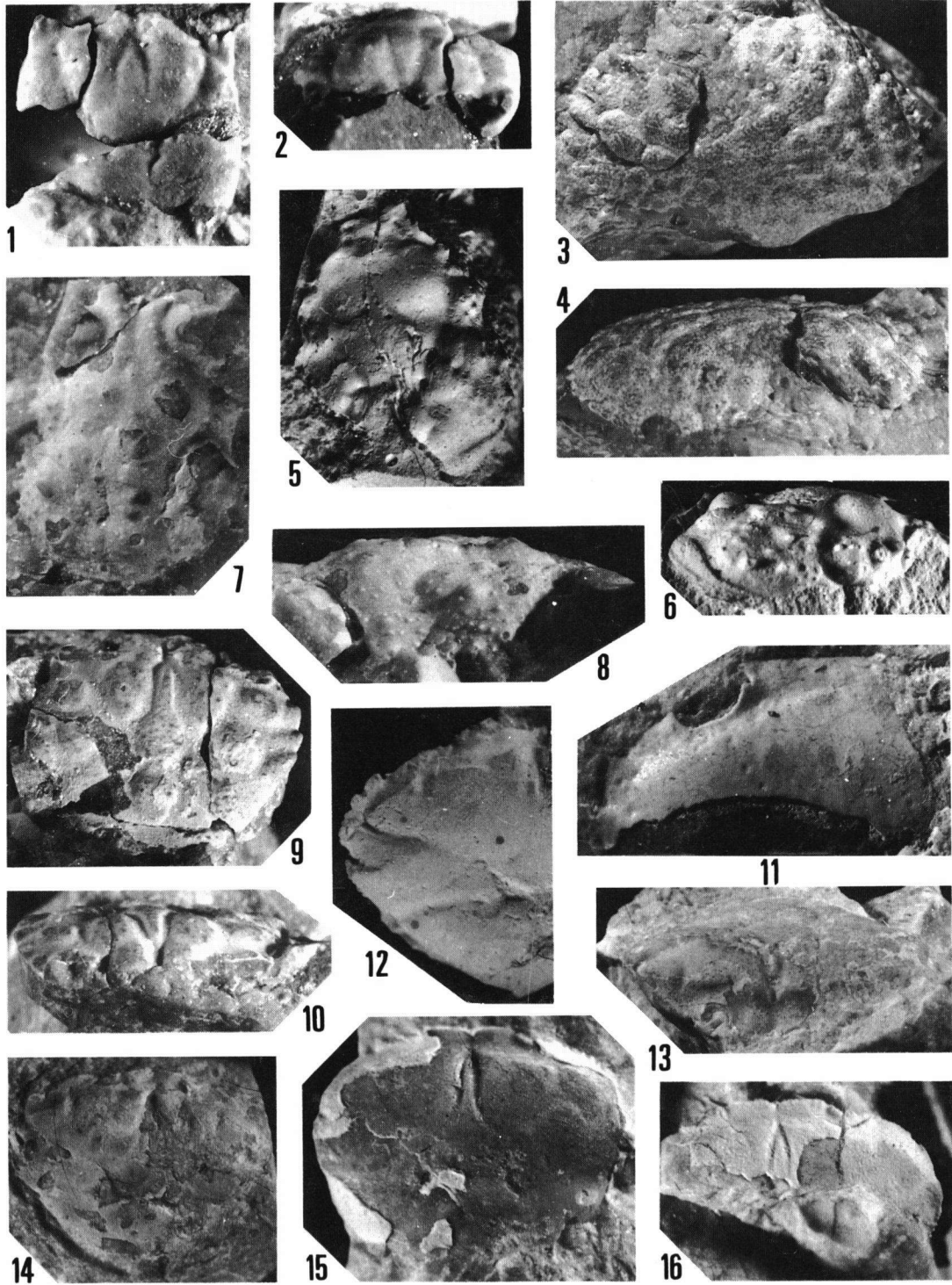
- 1905 *Gemmellarocarcinus loerentheyi* Checchia-Rispoli, p. 316, pl. 1, figs 1, 2.
- 1969 *Gemmellarocarcinus loerentheyi* Checchia-Rispoli — Via, p. 379.
- 1975 *Gemmellarocarcinus loerentheyi* Checchia-Rispoli — Müller, pp. 510, 516.

*New material* — Carapaces EK-9.1-3 [M.91-141] and EGA-8.1 [M.91-142].

PLATE 4

- Figs 1, 2     *Ethusa evae* sp. nov., 1 - dorsal view of carapace, holotype, EF-13.1 [M.91-144], x 9.2; 2 - frontal view of carapace, EF-13.1 [M.91-144], x 9.2.
- Figs 3, 4     *Daira eocaenica* (Lörenthey), 3 - dorsal view of carapace, EF-16.2 [M.91-160], x 5.7; 4 - frontal view of carapace, EF-16.2 [M.91-160], x 5.7.
- Figs 5, 6     *Nanomaja simplex* gen. et sp. nov., 5 - dorsal view of carapace, holotype, EBA-9.1 [M.91-149], x 7.8; 6 - frontal view of carapace, EBA-9.1 [M.91-149], x 7.8.
- Figs 7, 8     *Micromaia batalleri* Via, 7 - dorsal view of latex of carapace, EF-15.1 [M.91-146], x 8.7; 8 - frontal view of latex of carapace, EF-15.1 [M.91-146], x 8.7.
- Figs 9, 10    *Actaeites lobatus* gen. et sp. nov., 9 - dorsal view of carapace, holotype, EF-22.1 [M.91-153], x 6; 10 - frontal view of carapace, EF-22.1 [M.91-153], x 6.
- Fig. 11     *Neptocarcinus millenaris* Lörenthey, showing details of the front and orbit, EF-32.2 [M.91-152], x 6.8.
- Figs 12-14    *Paraxanthosia budensis* gen. et sp. nov., 12 - dorsal view of carapace, holotype, EK-18.1 [M.91-168], x 4.8; 13 - frontal view of carapace, EK-18.2 [M.91-168], x 3.3; 14 - dorsal view of carapace, EK-18.2 [M.91-168], x 3.3.
- Figs 15, 16    *Budapanopeus denticulatus* gen. et sp. nov., 15 - dorsal view of carapace, holotype, EK-17.1 [M.91-155], x 5.8; 16 - dorsal view of carapace, EK-17.2 [M.91-155], x 5.4.

PLATE 4



*Remarks* — This species has much in common with *Cyamocarcinus*; the outline of the carapace, the orbitofrontal region and the form of the cervical and postcervical furrows coincide in both species and are well comparable to analogous features of *Dynomene* Latreille in Desmarest, 1825.

Genus *Ovamene* gen. nov.

*Derivation of name* — From the ovate outline of the carapace and the generic suffix *Dynomene*.

*Type species* — *Ovamene francae* sp. nov.

*Diagnosis* — Carapace longitudinally subovate, the front takes up half of the orbitofrontal margin; the cervical furrow is medially V-shaped and a small intestinal lobe is present.

***Ovamene francae* sp. nov.**

Pl. 3, Fig. 7; text-fig. 3i

*Derivation of name* — From Francia, the type locality.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-12.1 [M.91-143]).

*Description* — The carapace is longitudinally subovate, breadth about three fourths of the length, widest about midlength; longitudinally and transversely flatly arched. The anterolateral margins are rounded and sharply turned inwards. A thin ridge developed on the posterolateral margins continues round acute posterior angles and concave posterior margin which is as wide as the orbitofrontal margin. The orbitofrontal margin occupies about half of the carapace width and is typically dynomenid; in frontal view it appears as a sloping, nearly straight line starting from the apex and turning down as an almost circular curve, forming the orbit. The rostrum-like triangular front is bent gently upwards and produced a little beyond the orbits; its sides are weakly upturned. The cervical furrow is acutely V-shaped where it crosses the midline about mid-carapace length, on the internal mould it is seen to curve forwards and outwards to the margin. The cardiac region is pentagonal, laterally defined by broad, hachured furrows and a smooth furrow separates it from an ovate intestinal lobe. The dorsal surface is smooth.

*Discussion* — There is in the triangular front and median portion of the cervical furrow some resemblance to the Late Cretaceous *Graptomacarcinus texanus* Roemer, 1887, but the latter is transversely ovate and lacks the intestinal lobe.

Superfamily Dorippoidea de Haan, 1833

Family Dorippidae de Haan, 1833

Genus *Ethusa* Roux, 1830

*Type species* — *Ethusa mascarone* (Herbst, 1785), by subsequent designation of Fowler (1912). Range: Late Eocene-Recent.

***Ethusa evae* sp. nov.**

Pl. 4, Figs 1, 2; text-fig. 3h

*Derivation of name* — The species is named after Mrs Éva Müller.

*Diagnosis* — Carapace subquadrate in outline, not much longer than wide with flattened nodes on the hepatic, gastric and cardiac regions.

*Material* — Holotype, a carapace (EF-13.1 [M.91-144]).

*Description* — The carapace is subquadrate in outline, widest at its posterior fifth and fractionally longer than broad. In longitudinal section the front, as far as the tip of the anterior mesogastric process, is flatly depressed, rising steeply to the mid-gastric region it becomes almost flat to the posterior margin, transversely it is almost flat with the lateral edges well rounded. The wide orbitofrontal margin is not well preserved; forward facing orbits appear to occupy the corners, and the front is produced beyond well-developed curving outer orbital spines, behind which is a vague constriction and short gently convex anterolateral margins terminate at a feeble cervical notch. The posterolateral margins, also gently convex, diverge only slightly towards the posterior margin. A shallow cervical furrow crosses the midline about mid-carapace length in a broad V, curving sharply forwards and outwards, it unites with the hepatic furrow then turns sharply out to the margin; the hepatic furrow continues the former curve and reaches the front close to the outer orbital spine. The branchiocardiac furrow is wider and deeper than the cervical furrow; from a more prominent marginal notch, it runs smoothly to the widest part of the cardiac region and is bounded behind by a weak ridge. The very small, lozenge-shaped mesogastric lobe has a transverse pair of weak nodes, its anterior process is broad and parallel sided for half its length before curving to the apex at a sharp angle. There is a large flattened node on each protogastric lobe and these form a shallow curve with a smaller one on each hepatic region. There appears to be one, perhaps two, bluntly rounded marginal spines on each epibranchial lobe; the

lobe itself is weakly tumid and confluent with a narrow mesobranchial lobe which is separated from a short, bar-like urogastric lobe and anterior part of the cardiac region by deep epimeral adductor muscle scars. Only the anterior part of the cardiac region is seen and this has a transverse pair of nodes.

*Discussion* — In its somewhat wide outline *E. evae* resembles the Late Cretaceous (Maastrichtian) *Binkhorstia ubaghzi* (Binkhorst, 1857), but differs in having a well-defined mesogastric lobe, a distinct urogastric lobe and the hepatic furrows approach the front closer to the outer orbital angles, thus reducing the size of the hepatic regions. All the above surface characters are to be found in *Ethusa* and the fact that the carapace is relatively wider anteriorly than apparent in Recent species hardly disbars the new species from this genus. Among Recent species *Ethusa mascarone americana* Rathbun, 1898, at least, has low tubercles or nodes on the gastric, hepatic and cardiac regions. Extant *Ethusa* spp. are generally reported from non-reefal localities; Müller (1984b) reported *E. mascarone* Herbst, probably a subspecies, from a Messinian reef at Santa Pola, Spain.

Superfamily Leucosioidea Samouelle, 1819  
 Family Leucosiidae Samouelle, 1819  
 Genus *Gemmacarcinus* gen. nov.

*Derivation of name* — The Latinised form of Bimbò (ùt), the type locality, and the suffix *-carcinus*.

*Type species* — *Gemmacarcinus fossatus* sp. nov.

*Diagnosis* — A wide subhexagonal carapace with deep furrows delimiting extremely convex regions.

***Gemmacarcinus fossatus* sp. nov.**

Pl. 3, Fig. 13; text-fig. 3j

*Derivation of name* — Referring to the deep furrows delimiting the extremely convex regions, the front is narrow and protruding.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EBA-8.1 [M.91-145]).

*Description* — The carapace is rounded-hexagonal in outline; the lateral margins are imperfectly preserved but the length was probably about two thirds of the width; transversely moderately convex laterally, longitudinally it is rather more steeply rounded in front. Small circular orbits are set close to the front which takes up one fourth of the carapace width; it

is produced, nearly straight with rounded corners and divided medially by a deep U-shaped notch. The marginal edge is rounded and numerous spinules line the broadly convex anterolateral margins; convexi-concave posterolateral margins converge by acute posterior angles to a posterior margin somewhat wider than the front. For the most part the regions and lobes are well defined and tumid and the cervical groove is particularly noticeable in its lateral course. The mesobranchial is the least prominent of the lobes and elongate-oval in outline, its very narrow anterior process tapers to the base of subquadrate epigastric lobes. The urogastric lobe and cardiac region are ovate and progressively wider than the mesogastric lobe. The branchial, hepatic and intestinal regions are delimited by deep furrows. Traces of the shell are preserved on both the internal and external moulds. There is a small node about the middle of each protogastric lobe and similar ones occupy the outer angles of the intestinal region. Small, evenly distributed tubercles cover the dorsal surface. Scattered remnants of these tubercles are seen as small pits on the decorticated carapace — a typical leucosiid-like structure.

*Discussion* — The narrow protruding front with small orbits at its base is a common feature of the Leucosiidae, although leucosiids seldom have such deep furrows as *Gemmacarcinus fossatus*. A, probably superficial, pattern of grooves can be seen in some *Randallia* species such as *Randallia pustuloides* Sakai, 1961. *Merocryptus lambriformis* A. Milne Edwards, 1873 has a similar carapace outline, but the regions are delimited quite differently. The narrow bifid front also shows some similarities to that found in the xanthid genus *Hepatoporus* Serène, 1984 and the deep cervical furrow of *G. fossatus* delimits tumid branchial and gastric regions in much the same way as in *Hepatoporus guinotae* (Zarenkov, 1971) from the Indo-Pacific, without showing the cavity at the hepatic region seen in that species. Surface features of *G. fossatus* have much in common with members of *Osachila* Stimpson, 1871, but *Osachila* has sharp margins, whereas *G. fossatus* has rounded ones. Guinot (1966) remarked that *Osachila* is a member of a group which is transitional between Parthenopidae and the Oxystemata with leucosiid affinities. *Gemmacarcinus fossatus* evidently forms an early step in this transition and Guinot's (1966) remarks, together with the leucosiid propensities mentioned above have influenced us in placing this species in the Leucosiidae, at least for the time being. Previous references to *Osachila trechei* Studer, 1898, are not

applicable because that species is actually an *Atelecyclus*.

Section Oxyrhyncha Latreille, 1803  
Family Majidae Samouelle, 1819  
Genus *Micromaia* Bittner, 1875

*Type species* — *Micromaia tuberculata* Bittner, 1875, by monotypy. Range: Eocene.

***Micromaia batalleri* Via, 1959**

Pl. 4, Figs 7, 8

1959 *Micromaia batalleri* Via, p. 373, fig. 12.

1969 *Micromaia batalleri* Via — Via, pp. 169, 394, pl. 11, figs 11, 12.

*New material* — Carapaces, EF-15.1-2 [M.91-146].

*Remarks* — Although only about half the size, the Szépvölgy specimens (kindly examined by Dr Via) are identical with the types from the Middle Lutetian of Catalonia, Spain.

Genus *Nanomaja* gen. nov.

*Derivation of name* — Alluding to the small size and possible relationship to *Micromaia*.

*Diagnosis* — Carapace arched in transverse and longitudinal sections; five marginal spines on the branchial margin, one of them at the lateral angle; the gastric regions are smooth, the hepatic and branchial regions are granulate.

*Type species* — *Nanomaja simplex* sp. nov.

***Nanomaja simplex* sp. nov.**

Pl. 4, Figs 5, 6; text-fig. 3d

*Derivation of name* — Alluding to the relatively unornamented carapace.

*Diagnosis* — As for genus.

*Material* — Holotype, external mould of a carapace (EBA-9.1 [M.91-149]), and paratypes, carapaces (EF-14.1-3 [M.91-147], EK-12.1-10 [M.91-148], EBA-9.2-7 [M.91-149]).

*Description* — The carapace is subpyriform in outline with tumid lobes and deep furrows; flatly arched longitudinally, slightly depressed at the urogastric lobe and highest at the cardiac region; it is slightly arched transversely, rising in lateral and median arcs. The length excluding the rostrum is slightly more than twice the greatest width which occurs about four fifths distant from the front. The rostrum is poorly preserved, but was probably bifid with

short blunt spines. The orbits are small and circular. There is a small rounded preocular spine at the base of the rostrum, a similar one lies over the orbit and between them, set slightly lower, is a smaller spine at the antennal septum. The base of a broken (postocular) spine suggest it to have been the stoutest. There is a similar basal scar on the almost circular hepatic region. The boldly curving metabranchial lobe overhangs the true lateral margin and has three granular spines in line close to the cervical notch, followed by two larger spines, the second set at the lateral angle. The true lateral margin, seen only near the posterior margin is bounded by a ridge expanding posteriorly and terminating close to a small intestinal lobe. The posterior margin is not preserved. The cervical furrow is nearly straight where it crosses the midline coincident with greatest carapace width, becoming deeper it curves sharply towards the anterior border of the mesogastric lobe then turns sharply out to a notch in the lateral margin. The proto-hepatic furrow continues the forward curve of the cervical furrow to the outer orbital angle. A much shallower and broader branchiocardiac furrow curves from the urogastric lobe to the cervical notch and isolates the epibranchial lobes from the margin. At the base of the rostrum small epigastric lobes have a granule at their distal border. Large, rounded protogastric lobes are separated by the slender anterior process of the pentagonal mesogastric lobe. The urogastric lobe is small, ovate and depressed. There is a transverse pair of nodes on the cardiac region and a node between the cardiac region and each metabranchial lobe. The epi- and mesobranchial lobes are weakly separated from one another and partially divided by a groove following the curve of the branchial furrow. Small spiny granules of several diameters ornament the hepatic and branchial regions, the gastric lobes are smooth.

*Discussion* — *Nanomaja* has some similarities with *Micromaia* (see Beschin *et al.*, 1985) especially about the orbitofrontal region and in the carapace outline, but *Micromaia* lacks the posterior marginal ridge developed in *Nanomaja* and has a dense array of tubercles (except *Micromaia laevis* Lörenthey, 1909, which seems quite different from other species of this genus).

The general arrangement of the orbital spines, the presence of spines on the branchial margin — with one at the lateral angle — the course of the furrows and the large rounded protogastric lobes point to a strong relationship with the Recent

*Microphrys* Milne Edwards, 1851, but the absence of the rostrum and antennal characters of the new species, makes finite comparison uncertain.

Majidae sp. 1

*Material* — Internal and external moulds of a carapace, EK-36.1 [M.91-150].

*Description* — The moderately convex carapace is pyriform in outline, posteriorly widely elliptical because of semicircular branchial regions. Deep furrows delimit the subhexagonal cardiac region which has a transverse pair of nodes. Furrows delimit the meta-, meso- and epibranchial lobes. There is a tubercle on the mesogastric lobe, four on the meso- and five or six on the metabranchial lobes.

*Remarks* — This specimen differs from *Micromaia batalleri* in having a much smoother surface and two distinct nodes on the cardiac region rather than one, albeit double pointed, tubercle. Most other *Micromaia* spp. are even more tuberculated than *M. batalleri*. The carapace width distinguishes EK-36.1 from *Nanomaja*. The specimen is insufficiently well preserved, however, to give it specific status.

Family Parthenopidae Macleay, 1838  
Genus *Mesolambrus* gen. nov.

*Derivation of name* — *Meso-* from the mesobranchial lobe and the generic group root.

*Type species* — *Mesolambrus declinatus* sp. nov.

*Diagnosis* — Carapace steeply downturned anteriorly, the orbits are large with weak upper margins; regions well defined with the epi- and mesobranchial lobes distinct; the dorsal surface is coarsely tuberculated.

***Mesolambrus declinatus* sp. nov.**

Pl. 3, Figs 11, 12, ?14-17; text-fig. 3f

*Derivation of name* — From the downturned orbito-frontal region.

*Diagnosis* — As for genus.

*Material* — Holotype, a decorticated carapace, EGA-9.1 [M.91-151] and paratype, a carapace fragment, EGA-9.2 [M.91-151].

*Description* — The carapace is subpentagonal in outline, length about half the width, widest about three fifths distant from the front. It is steeply arched transversely, longitudinally it rises steeply from the front to the fore-edge of the epigastric lobes, slants back to the cardiac region and curves to the poste-

rior margin. The orbits, directed slightly obliquely, take up the outer fourths of the orbitofrontal margin. The front is damaged, but probably slightly produced, medially depressed with the raised edges granulated; the depression continues back as a deep trough widely separating the epigastric lobes. The upper orbital margin is thin, slightly raised and has a notch before the outer orbital spine. Behind this spine is the base of a smaller spine which is followed by a stouter one. Rounded posterolateral margins are slightly raised and have the bases of three tubercles or nodes. The cervical furrow is shallow and nearly straight where it crosses the midline some three fourths distant from the front then runs forwards and outwards round protuberant mesobranchial and epibranchial lobes. The epibranchial lobes form rounded ridges divided into three nodes of which the median is the largest, the mesobranchial lobe lies between the innermost node and the anterior angle of the cardiac region. On each protogastric lobe are two nodes and in front of these three tubercles are arranged in a semicircle, the median one occurring immediately behind slightly larger epigastric lobes. The anterior mesogastric process extends to the middle of the three protogastric tubercles and itself has three tubercles, the median one the largest. A small rectangular urogastric lobe is depressed and less clearly separated from the mesogastric lobe than from the heart-shaped cardiac region.

Internal moulds of three propodi, EK-11.1-3 (Pl. 3, Figs 14-17) are typically parthenopid and may possibly belong to *Mesolambrus*; they are subpentagonal in cross section distally, becoming ovate proximally, a little higher than wide. There is an acute angle on either side of the basal margin with the surface between nearly flat. The outer surface is convex and has a rounded median ridge and an acute distal one. The upper margin is obliquely inclined, the inner margin is concave in its upper fourth where there is a ridge, then almost straight to the basal margin. Each ridge has four or five evenly spaced spines and numerous spiny granules crowd the interridge spaces.

The limbs are not far distant from those described as *Andorina elegans* by Lörenthey in 1929, but correctly assigned to *Parthenope* by Müller (1984a). The upper margin on Lörenthey's figure is more sharply inclined and the ridge on the outer margin is subdued producing a more quadrilateral effect. There is also the possibility of the limbs belonging to *Phry-nolambrus corallinus* Bittner, 1893 occurring in Facies

5 of the Szépvölgy Limestone, but of which no evidence has so far been found in Facies 4.

*Discussion* — Among Recent parthenopids *Mesolambrus* has a marked similarity to *Thyrolambrus* Rathbun, 1894; it differs largely in the presence of weakly developed upper orbital margins and distinct mesobranchial lobes which on *Thyrolambrus* are displaced laterally and more or less fused with the epibranchial lobes leaving the resulting space between them and the cardiac region as a depression. The isolated mesobranchial lobe and prominent anterior mesogastric process readily distinguish *Mesolambrus* from *Parthenope* Weber, 1795 and *P. (Platylambrus)* Stimpson, 1871. Furthermore the branchial ridge on the latter (sub)genera is usually entire, not broken by tubercles as in *Mesolambrus*.

Section	Brachyrhyncha Borradaile, 1907
Superfamily	Portunoidea Rafinesque, 1815
Family	Portunidae Rafinesque, 1815
Genus	<i>Neptocarcinus</i> Lőrenthey, 1897

*Type species* — *Neptocarcinus millenaris* Lőrenthey, 1897, by monotypy. Range: Late Eocene.

*Remarks* — Lőrenthey (1898a, b) ranged *Neptocarcinus* among Cancrinae emphasising its similarity to 'Nep-tunus'. In 1929 Lőrenthey (in Lőrenthey & Beurlen) transferred the species to Xanthidae, a view accepted by Busulini *et al.* (1983). We exclude *Neptocarcinus* (= *Coralliocancer*) *spinus* and *Prochlorodius ellipticus* from this genus, for reasons given below. The remaining true *Neptocarcinus* (*N. millenaris*), as far as it possible to judge from the carapace surface, shows much stronger affinities to portunids than to other brachyuran families. The form of its carapace readily brings to mind that of *Catopterus* A. Milne Edwards, 1870, *Libystes* A. Milne Edwards, 1867, *Carupa* Dana, 1851 and *Rakosia* Müller, 1984a.

### ***Neptocarcinus millenaris* Lőrenthey, 1897**

Pl. 4, Fig. 11; text-fig. 4a

- 1897 *Neptocarcinus millenaris* Lőrenthey, p. 156.  
 1898b *Neptocarcinus millenaris* Lőrenthey — Lőrenthey, p. 179, pl. 4, fig. 3.  
 1969 *Neptocarcinus millenaris* Lőrenthey — Via, p. 298 (see also for synonymy).  
 1975 *Neptocarcinus millenaris* Lőrenthey — Müller, pp. 516, 520.  
 1983 *Neptocarcinus millenaris* Lőrenthey — Busulini *et al.*, p. 66, pl. 3, fig. 3.

*Material* — Lőrenthey's specimens are in the collection of MÁFI. Lectotype designated herein: Lőren-

they, 1898b, pl. 4, fig. 3; new material: carapaces EF-32.1-8 [M.91-152].

*Remarks* — Nothing new can be added to the original description.

Superfamily	Xanthoidea Dana, 1851
Family	Xanthidae Dana, 1851
Genus	<i>Actaeites</i> gen. nov.

*Derivation of name* — With reference to the similarity to *Actaea* de Haan, 1833.

*Type species* — *Actaeites lobatus* sp. nov.

*Diagnosis* — Carapace almost circular with five pairs of lateral spines and a wide orbitofrontal margin, the regions are distinct and the epibranchial lobe has two short ridges.

### ***Actaeites lobatus* sp. nov.**

Pl. 4, Figs 9, 10; text-fig. 4c

*Derivation of name* — Referring to the well-defined surface characters.

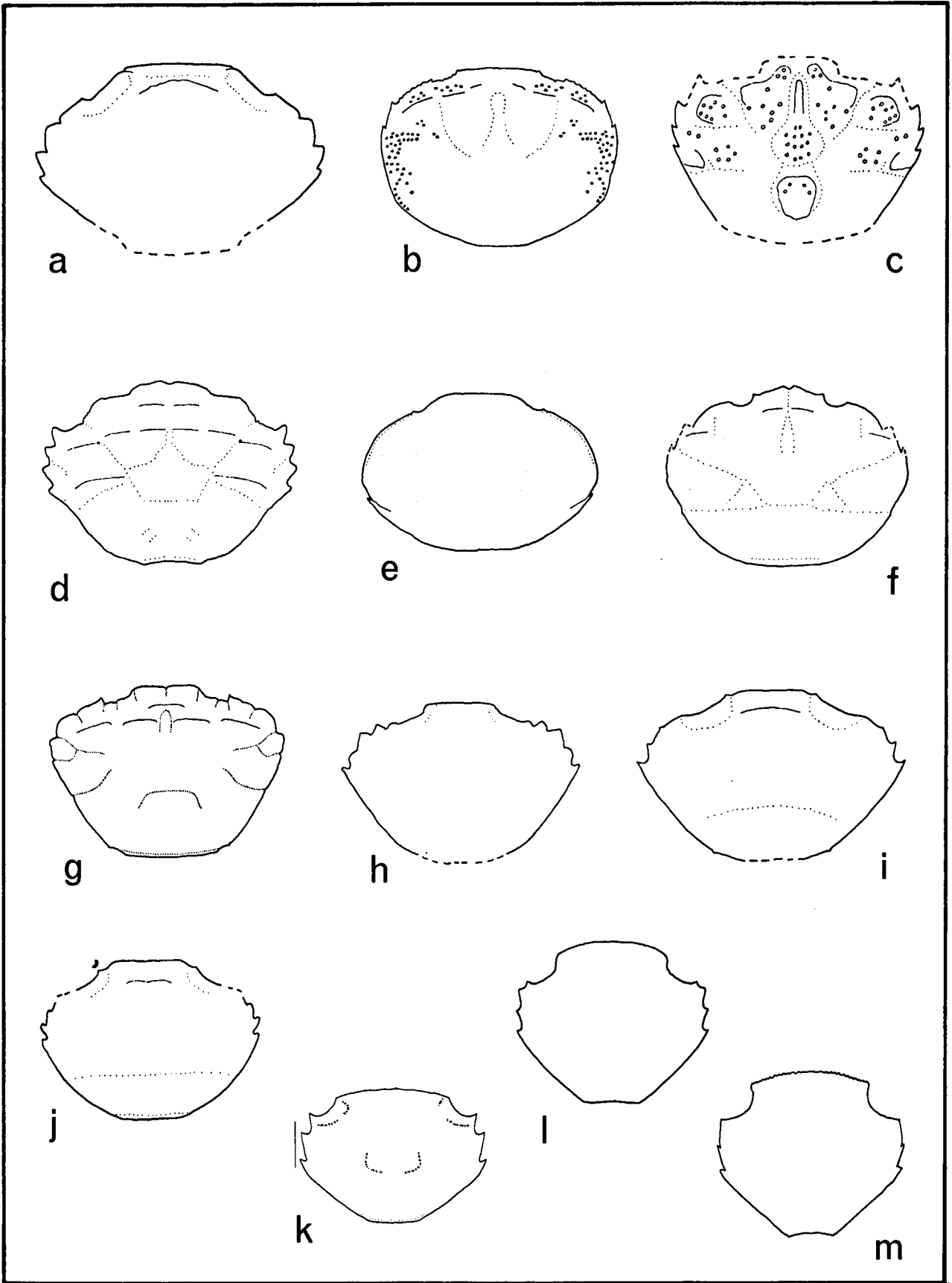
*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-22.1 [M.91-153]).

*Description* — The carapace is almost circular in outline, widest a little anterior to midlength; longitudinally gently arched, but rather more steeply downturned in front, and moderately arched transversely. Thin anterolateral edges over-reach the straight sides. The orbitofrontal margin takes up almost the entire carapace width and the orbits occupy the outer thirds. A sharp outer orbital spine is followed by an upturned one anterior to the cervical notch; behind the notch two spines close together lead back to posteriorly directed ridges on the epibranchial lobe and the 4th and 5th spines are reduced in size. The posterolateral margins converge to the posterior margin which is narrower than the front. A V-shaped notch divides the front into two rounded slightly produced lobes and thin, slightly raised upper orbital margins are pierced by

Fig. 4. Diagrammatic views of: a - *Neptocarcinus millenaris* Lőrenthey, b - *Budapanopeus denticulatus* gen. et sp. nov., c - *Actaeites lobatus* gen. et sp. nov., d - *Panopeus granulineatus* sp. nov., e - *Priabonocarcinus gallicus* gen. et sp. nov., f - *Paraxanthosia budensis* gen. et sp. nov., g - *Laevicarcinus egerensis* Lőrenthey, h - *Pilumnomimus planidentatus* gen. et sp. nov., i - *Prochlorodius ellipticus* gen. et sp. nov., j - *Prochlorodius ellipticus*, juvenile, k - *Eomaldivia pannonica* gen. et sp. nov., l - *Eomaldivia trispinosa* gen. et sp. nov., m - *Tetralia loerentheyi* (Müller).





two notches. Well-defined regions are slightly tumid and finely granulated. The cervical furrow extends almost straight across the midline about mid-carapace length, turns sharply out to meet the protogastric furrow then curves round the hepatic region to the margin. A fine groove isolates the circular hepatic regions from the margin. The anterior mesogastric process is attenuated between moderately large epigastric lobes. The mesogastric, triangular urogastric and ovate cardiac regions are divided by a median furrow and there is a small node between the cardiac region and the mesobranchial lobes. *Discussion* — The well-defined lobes and their disposition on *Actaeites* much resembles several species of the old genus *Actaea* de Haan, 1833, now split into numerous genera. A much wider orbitofrontal margin, bigger orbits and a wider anterior sub-lobe of the mesogastric lobe, however, readily distinguishes *Actaeites* from *Actaea*, *Novactaea* Guinot, 1976, *Epiactaea* Serène, 1984, *Forestia* Guinot, 1976 or related extant genera. The general outline and distribution of the lobes also resembles some members of *Lophopanopeus* Rathbun, 1898; *Actaeites* differs in having a wider orbitofrontal margin, in the juxtaposition of the anterolateral spines and in the absence of frontal lobes generally present in *Lophopanopeus*.

Genus *Budapanopeus* gen. nov.

*Derivation of name* — From Buda, type locality and the related genus *Panopeus*.

*Type species* — *Budapanopeus denticulatus* sp. nov.

*Diagnosis* — Carapace elliptical, front straight with a median notch, step-like postfrontal and hepatic ridges transversely aligned.

***Budapanopeus denticulatus* sp. nov.**

Pl. 4, Figs 15, 16; Pl. 5, Figs 2, 7, 14; text-fig. 4b

*Derivation of name* — Alluding to the marginal denticulation.

*Diagnosis* — As for genus.

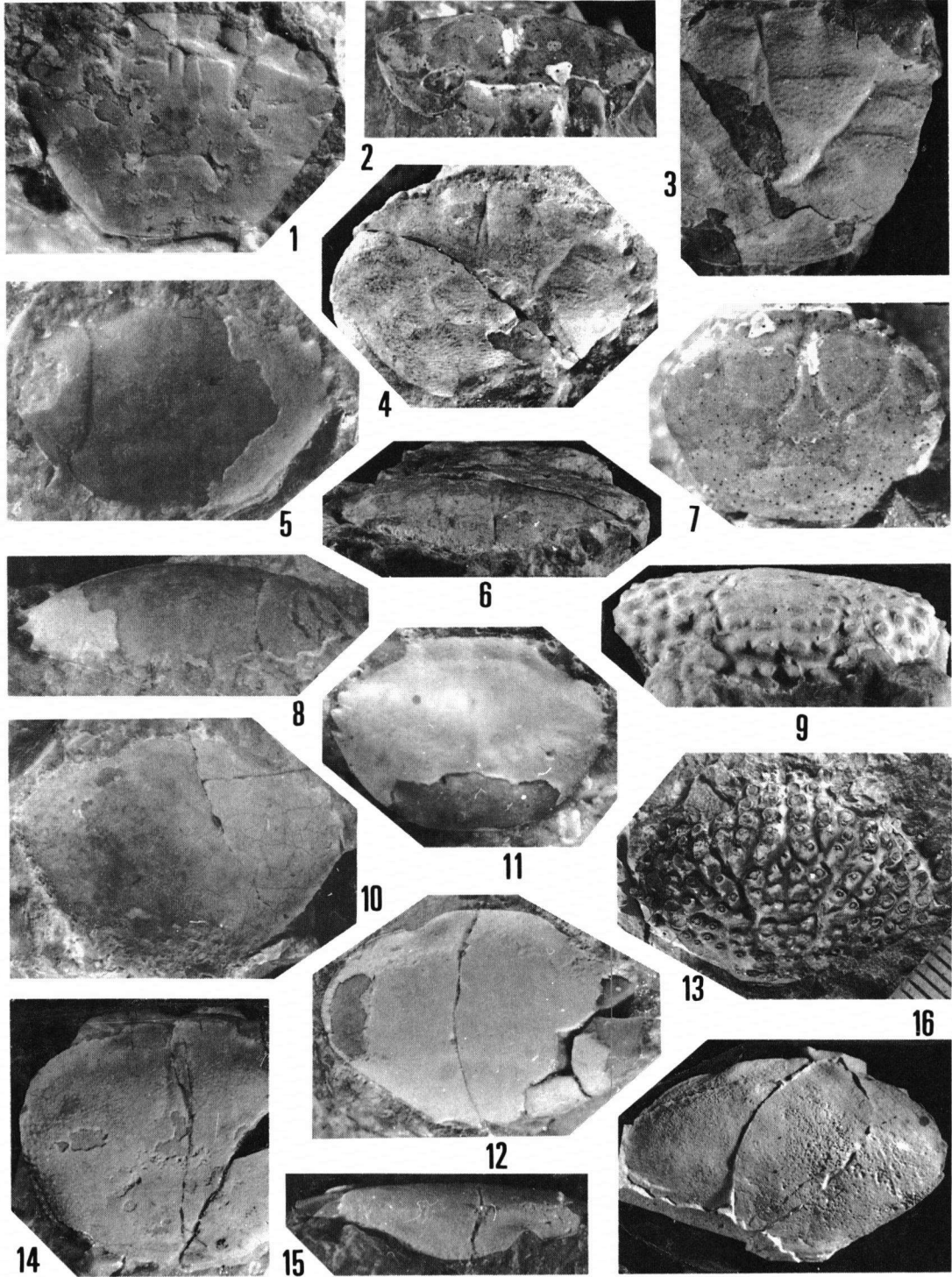
*Material* — Holotype, a carapace (EK-17.1 [M.91-155]) and paratypes (EK-17.2-14 [M.91-155], EF-17.1-3 [M.91-154], EGA-21.1-5 [M.91-158], EGF-6.1-2 [M.91-159], EBA-12.1 [M.91-156], EBV-7.1 [M.91-157]).

*Description* — The subelliptical carapace has well-rounded anterolateral margins forming an almost continuous curve with the frontal margin; the length is about four fifths of the width. Longitudinally it rises steeply from the front, curves into a depression behind the epibranchial lobes and is convex from the cardiac region posteriorly; it is moderately arched transversely. Even sized granules line the anterolateral margins and, becoming finer, continue across the front. The produced front takes up rather more than half of the orbitofrontal margin which occupies about four fifths of the carapace width; there is a median notch and the sides are nearly straight. Deep notches separate the upper orbital margins from the front and anterolateral margins. Broadly curved where it crosses the carapace posterior to midlength, the cervical furrow curves outwards at its junction with the protogastric furrow, unites with the hepatic furrow, and recurves round the large, ovate hepatic regions. The hepatic furrow continues the original curve of the cervical furrow to the front. A groove extending from the median frontal depression divides and isolates the anterior mesogastric process. Step-like ridges on the

PLATE 5

- Fig. 1 *Laevicarcinus egerensis* Lörenthey, dorsal view of carapace, holotype, Eger, MAFI Coll., x 2.9.  
Figs 2, 7, 14 *Budapanopeus denticulatus* gen. et sp. nov., 2 - frontal view of carapace, paratype, EF-17.1 [M.91-155], x 5.9; 7 - dorsal view of carapace, EF-17.1 [M.91-155], x 5.9; 14 - dorsal view of carapace, paratype, EBA-12.1 [M.91-156], x 6.2.  
Figs 3, 4, 6 *Panopeus granulineatus* sp. nov., 3 - dorsal view of carapace showing details of the front and linear ridges on right side, paratype, EGA-11.2 [M.91-167], x 4.9; 4 - dorsal view of carapace, EGA-11.1 [M.91-167], x 2.1; 6 - frontal view of carapace, holotype, EGA-11.1 [M.91-167], x 2.1.  
Figs 5, 8, 10 *Pilumnomimus planidentatus* gen. et sp. nov., 5 - dorsal view of carapace, paratype, EGA-16.1 [M.91-171], x 5.4; 8 - frontal view of carapace, EGA-16.1 [M.91-171], x 5.4; 10 - dorsal view of carapace, holotype, EK-35.1 [M.91-170], x 4.5.  
Fig. 9 *Phlyctenodes krenneri* Lörenthey, frontal view of carapace, EGF-9.1 [M.91-178], x 5.  
Fig. 11 *Prochlorodius ellipticus* gen. et sp. nov., dorsal view of juvenile carapace, paratype, EK-28.1 [M.91-183], x 11.  
Figs 12, 15, 16 *Priabonocarcinus gallicus* gen. et sp. nov., 12 - dorsal view of carapace, holotype, EF-25.1 [M.91-180], x 5.4; 15 - frontal view of carapace, EF-25.1 [M.91-180], x 5; 16 - dorsal view of latex of carapace, paratype, EF-25.2 [M.91-180], x 4.  
Fig. 13 *Phlyctenodes steinmanni* Lörenthey, dorsal view of carapace, Kissvábhegy, MÁFI Coll., x 2.

PLATE 5



hepatic and protogastric lobes are in line cross the front and the epi- and metabranchial lobes form well-rounded ridges. The sides of the rectangular urogastric and urn-shaped cardiac region are deeply embayed by prominent cuneiform pits formed by the epimeral adductor muscle scars.

*Discussion* — The genus shares characters with Eocene forms such as *Titanocarcinus* A. Milne Edwards, 1864 and *Pilumnoplax* Stimpson, 1858, in the outline and lobation of the carapace, but can be distinguished by the ridges on the hepatic, epi- and protogastric lobes. These ridges are present in *Paraxanthosia* gen. nov., *Panopeus* H. Milne Edwards, 1834 and *Laevicarcinus* Lórenthey in Lórenthey & Beurlen, 1929, but the more convex carapace of *Budapanopeus* gives it quite a different appearance; *Paraxanthosia* gen. nov. is further distinguished by its front and peculiar groove system.

Genus *Daira* de Haan, 1833

*Type species* — *Cancer perlatus* Herbst, 1790, by monotypy. Range: Late Eocene-Recent.

***Daira eocaenica*** (Lórenthey, 1897)

Pl. 4, Figs 3, 4

- 1897 *Phymatocarcinus eocaenicus* Lórenthey, p. 154.
- 1967 *Daira eocaenica* (Lórenthey) — Guinot, p. 550.
- 1969 *Daira eocaenica* (Lórenthey) — Via, p. 373 (see also for synonymy).
- 1975 *Daira eocaenica* (Lórenthey) — Müller, pp. 516, 520.
- 1979 *Daira eocaenica* (Lórenthey) — Guinot, p. 55.

*Material* — Type series in the collection of MAFI; new material: EF-16.1-7 [M.91-160], EF-15.1-3 [M.91-161], EGA-10.1 [M.91-163], EBA-10.1 [M.91-162].

*Remarks* — Guinot (1967) studied the genus and proposed its removal from the Xanthidae. Certainly, the relationship of *Daira* with other fossil decapods, including the apparently similar *Phlyctenodes*, deserves further study.

Genus *Laevicarcinus* Lórenthey & Beurlen, 1929

*Type species* — *Laevicarcinus egerensis* Lórenthey in Lórenthey & Beurlen, 1929, by subsequent designation of Glaessner (1929). Range: Late Eocene.

*Remarks* — Although placed in Carcinoplacidae by Lórenthey & Beurlen (1929) and in Carcinoplacinae by Glaessner (1969) the form and crests on the carapace suggest rather a *Panopeus*-affinity.

***Laevicarcinus egerensis*** Lórenthey in

Lórenthey & Beurlen, 1929

Pl. 5, Fig. 1; text-fig. 4g

- 1929 *Laevicarcinus egerensis* Lórenthey in Lórenthey & Beurlen, p. 238, pl. 11, fig. 8.
- 1969 *Laevicarcinus egerensis* Lórenthey & Beurlen — Via, p. 386.

*Material* — Holotype, a carapace (MAFI Coll.); paratype, a carapace fragment (MÁFI Coll.); new material: 3 carapaces, 2 chelae (EE-2.1-5 [M.91-164]), a carapace fragment J.S.H. Collins Collection 1659EE.

*Remarks* — The species is adequately described in Lórenthey & Beurlen (1929) but the figure (as almost all Lórenthey's posthumous figures, in striking contrast of those published during his lifetime) is very poor; the transverse section is elliptical, the chelae have the fixed finger quite stout and the surface is smooth. Crosnier & Guinot (1969) compared the species with *Platychelonion* Crosnier & Guinot, 1969 and Via (1969) related it to *Titanocarcinus*.

Genus *Panopeus* H. Milne Edwards, 1834

*Type species* — *Panopeus herbstii* H. Milne Edwards, 1834, by subsequent designation (ICZN Opinion no. 1282, 1984). Range: Palaeocene-Recent.

***Panopeus granulineatus*** sp. nov.

Pl. 5, Figs 3, 4, 6; text-fig. 4d

*Derivation of name* — With reference to the secondary surface ornament.

*Diagnosis* — Carapace subovate with four anterolateral spines and granule-lined steep fronted ridges on the epi- and protogastric lobes, hepatic region and epibranchial lobes.

*Material* — Holotype, a carapace (EGA-11.1 [M.91-167]) and paratypes, carapaces (EK-16.1-11 [M.91-165], EGA-11.2-11 [M.91-167], EBA-11.1-2 [M.91-166]).

*Description* — The subovate carapace is about one third broader than long, widest about midlength; moderately arched in longitudinal and transverse sections. There are four robust forwardly directed spines on the anterolateral margins, the fourth a little longer than the others. The front is of an uncommon shape; its median part, standing out from a broad base, is bilobed and its straight sides gently incline to a median U-shaped notch. Thus the whole front is very wide, occupying as much as

7/12ths of the carapace width. The cervical furrow crosses the midline about three fifths distant from the front, it is broad and deep to its junction with the protogastric furrow then turns outwards and runs in a broad shallow curve to reach the margin between the 3rd/4th spines. The protogastric furrow runs from between the 1st/2nd anterolateral spines towards the midline before turning sharply down to the cervical furrow. A triangular mesogastric lobe has a median basal depression and the tip of its narrow anterior process extends to the base of wide epigastric lobes. Steep-fronted ridges on the epigastric, protogastric and hepatic lobes are in echelon, those on the protogastric overlapping the epigastric ones by half their length and a curving ridge occurs on the epibranchial lobes. All the ridges are topped by fine granules. The urogastric and cardiac regions are confluent and lingulate. The surface ornament consists of numerous granules forming undulating, overlapping lines.

*Discussion* — The extremely wide front of uncommon shape and the four pairs of anterolateral teeth distinguishes *Panopeus granulineatus* from extant *Panopeus* species though the broad outline and ornament is typical for the genus.

Genus *Paraxanthosia* gen. nov.

*Derivation of name* — Indicating a relationship to *Xanthosia* Bell, 1863.

*Type species* — *Paraxanthosia budensis* sp. nov.

*Diagnosis* — Carapace subhexagonal with two epibranchial spines and a well-developed branchiocardiac furrow, short ridges occur on the hepatic and protogastric lobes.

***Paraxanthosia budensis* sp. nov.**

Pl. 4, Figs 12-14; text-fig. 4f

*Derivation of name* — From Buda, the type locality.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EK-18.1 [M.91-168]) and paratypes (EK-18.2-5 [M.91-168], ?EBA-18.1 [M.91-169]).

*Description* — The subhexagonal carapace is about twice as wide as long, moderately arched transversely and somewhat flattened in longitudinal section. The anterolateral margin is convex, the base of a spine is evident midway between the outer orbital and lateral angles. Of two thin, sharp spines on the epibranchial margin the first is the larger. The orbitofrontal margin is about half the width of the

carapace, the front is produced, triangular with a median notch and separated from the inner orbital angles by an incision. Sinuous posterolateral margins curve to the posterior margin which are about twice as wide as the front. From the margin the cervical furrow runs in a shallow curve behind the hepatic region, loops round the protogastric lobe and turns down more steeply round the mesogastric lobe; it crosses the midline some two thirds distant from the front and is interrupted medially by a thin extension from the urogastric lobe. Transverse branchiocardiac furrows are equally as deep as the cervical. Short ridges run parallel to the margin on the hepatic and protogastric lobes; there is a tubercle on each protogastric lobe and three in an inverted triangle on the cardiac region. A groove separates large epibranchial lobes from subdivided metabranchial lobe. On the side the hepatic and cervical furrows unite beneath the hepatic region and, curving forward, are joined by the branchiocardiac furrow and continue to the front.

*Discussion* — In having large epibranchial lobes with prominent spines, a median interruption of the cervical furrow, a deep branchiocardiac furrow and a pair of protogastric tubercles, this species contains many of the characters of the Cretaceous-Danian genus *Xanthosia* Bell, 1863 and, to a certain extent *Etyus* Mantell, 1822, also Cretaceous. The marginal edge of *Paraxanthosia* appears to be between the thin, somewhat upturned edge of *Xanthosia* and the rounded one of *Etyus*.

Genus *Pilumnomimus* gen. nov.

*Derivation of name* — From the Latin *mimus* -actor and *Pilumnus*.

*Type species* — *Pilumnomimus planidentatus* sp. nov.

*Diagnosis* — A strongly arched, smooth carapace, orbits well developed, frontal margin entire, four lobe-like anterolateral spines.

***Pilumnomimus planidentatus* sp. nov.**

Pl. 5, Figs 5, 8, 10; text-fig. 4h

*Derivation of name* — Alluding to the flattened, lobe-like marginal spines.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EK-35.1 [M.91-170]) and paratype, a carapace (EGA-16.1 [M.91-171]).

*Description* — The carapace is subhexagonal in outline, slightly rounded, about one fifth wider than

long, widest between the 2nd and 3rd lateral spines. In longitudinal section the anterior half forms almost a hemisphere, it is almost flat to the hinder three fourths and rounded again to the posterior margin; transversely, it is elliptical, being rather less convex medially than towards the lateral angles. The short curved anterolateral margins have four subequal flattened, lobe-like spines, separated from each other by deep incisions. The orbitofrontal margin takes up about four fifths of the carapace width. The orbits are wide with entire margins elevated near the inner orbital angles. There is a depression behind the front which is produced, its margins are entire, blunt and deflected. The posterolateral margins are strongly convergent, almost straight. No trace of regions is visible on the shell-surface. The internal mould of EGA-16.1 shows two shallow furrows delimiting the anterior mesogastric process and fainter furrows delimit the protogastric lobes. The dorsal surface is smooth anteriorly and covered in fine, densely crowded granules posteriorly.

*Discussion* — The form of the carapace is much like that of *Glabropilumnus* Balss, 1932 and other *Pilumnus*-related forms. These have a produced sharp-edged, lobated front which is generally a smooth continuation of the subglobular carapace surface. In *Pilumnomimus* the front is entire with an almost straight margin separated from the hinder parts by a depression. The smooth, convex carapace is similar to that of *Lobogalenopsis* (see below) but the genera differ in their anterolateral margins and the shape of the front.

Genus *Phlyctenodes* A. Milne Edwards, 1862

*Type species* — *Phlyctenodes tuberculatus* A. Milne Edwards, 1862, by subsequent designation of Glaessner (1929). Range: Middle Eocene-Oligocene.

**Phlyctenodes krenneri** Lörenthey, 1897

Pl. 5, Fig. 9; Pl. 6, Fig. 1

- 1897 *Phlyctenodes krenneri* Lörenthey, p. 154.
- 1905 *Phlyctenodes krenneri* Lörenthey — Checchia-Rispoli, p. 312, pl. 1, fig. 10.
- 1969 *Phlyctenodes krenneri* Lörenthey — Via, p. 408 (see also for synonymy).
- 1975 *Phlyctenodes krenneri* Lörenthey — Müller, pp. 516, 520.

*Material* — The holotype is in the collection of MÁFI. New material: EF-23.1-4 [M.91-172], EK-22.1-8 [M.91-173], EGA-15.1-2 [M.91-177], EGF-9.1-6 [M.91-178], EBA-17.1 [M.91-174], EBK-6.1-2 [M.91-175], EBV-3.1-3 [M.91-176].

*Remark* — Nothing further can be added to the original description.

**Phlyctenodes steinmanni** Lörenthey, 1901

Pl. 5, Fig. 13

- 1901a *Phlyctenodes steinmanni* Lörenthey, p. 815, pl. 1, fig. 4.
- 1901b *Phlyctenodes steinmanni* Lörenthey, p. 111, pl. 1, fig. 4.
- 1929 *Phlyctenodes steinmanni* Lörenthey — Lörenthey in Lörenthey & Beurlen, p. 200, pl. 12, fig. 2.

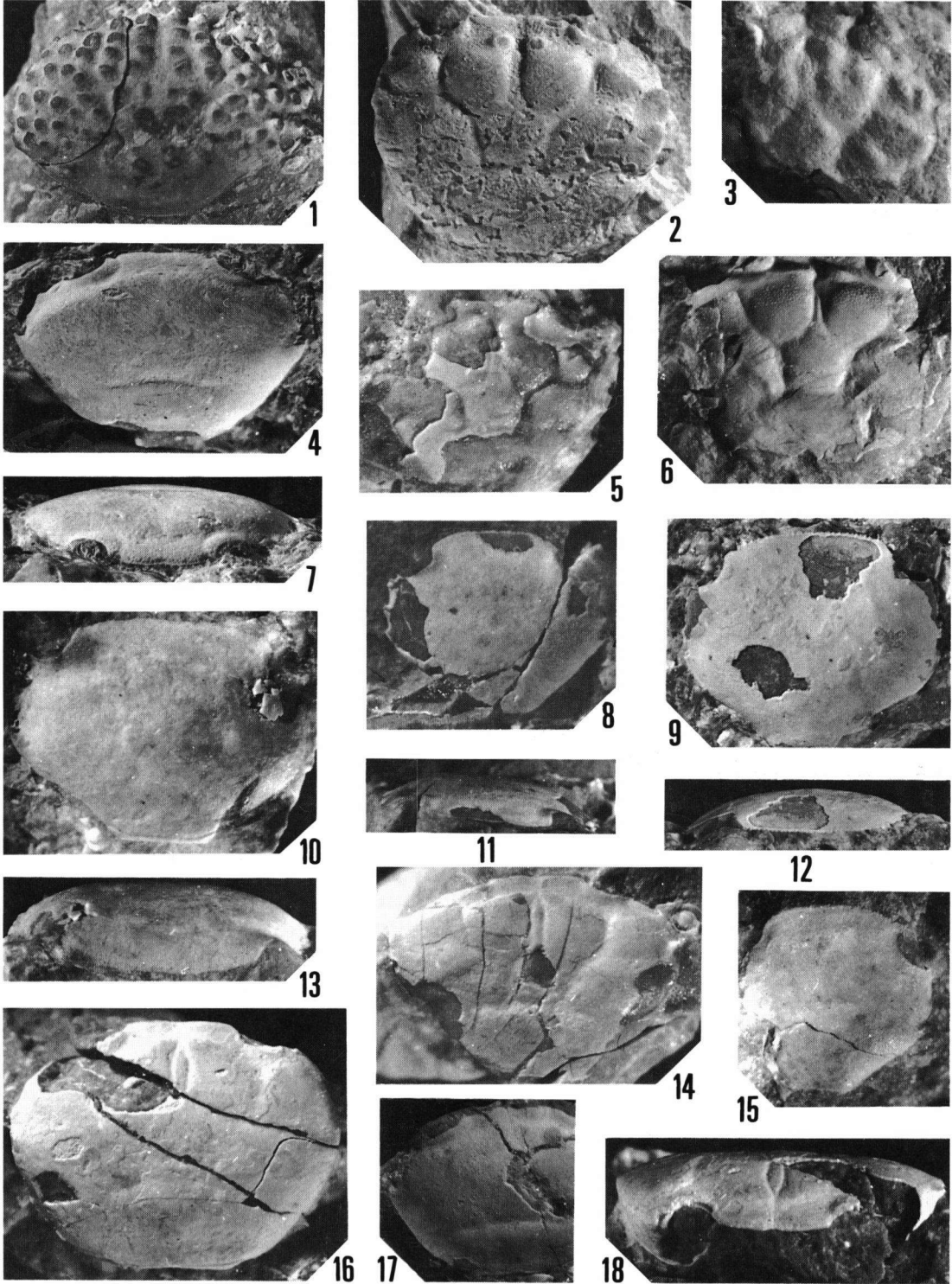
*Material* — The type series is in the collection of MÁFI. New material: two fragmentary carapaces (EGA-14.1-2 [M.91-179]).

*Remarks* — As Lörenthey's illustrations are only of damaged specimens we figure a specimen in the

PLATE 6

- Fig. 1 *Phlyctenodes krenneri* Lörenthey, dorsal view of carapace, EF-23.1 [M.91-172], x 5.2.
- Figs 2, 5, 6 *Titanocarcinus kochii* Lörenthey, 2 - dorsal view of carapace, Kissvábhegy, MÁFI Coll., x 2; 5 - dorsal view of carapace, EF-27.1 [M.91-187], x 3; 6 - dorsal view of carapace, EGF-11.1 [M.91-189], x 2.9.
- Fig. 3 *Syphax* sp., dorsal view of carapace, EK-23.1 [M.91-186], x 5.8.
- Figs 4, 7, 17 *Prochlorodius ellipticus* gen. et sp. nov., 4 - dorsal view of carapace, holotype, EF-20.1 [M.91-181], x 4.6; 7 - frontal view of carapace, EF-20.1 [M.91-181], x 4.6; 17 - dorsal view of carapace, paratype, EK-20.1 [M.91-182], x 6.
- Figs 8, 11 *Eomaldivia trispinosa* gen. et sp. nov., 8 - dorsal view of carapace, EF-19.1 [M.91-191], x 6.1; 11 - frontal view of carapace, EF-19.1 [M.91-191], x 6.1.
- Figs 9, 12, 15 *Tetralia loerentheyi* (Müller), 9 - dorsal view of carapace, EK-1.3 [M.91-194], x 6.8; 12 - frontal view of carapace, EK-1.3 [M.91-194], x 6.8; 15 - dorsal view of carapace, EF-18.1 [M.91-193], x 3.2.
- Figs 10, 13 *Eomaldivia pannonica* gen. et sp. nov., 10 - dorsal view of carapace, holotype, EGA-12.1 [M.91-190], x 6.5; 13 - frontal view of carapace, EGA-12.1 [M.91-190], x 6.5.
- Figs 14, 16, 18 *Branchioplax sulcata* gen. et sp. nov., 14 - dorsal view of carapace, holotype, EF-21.1 [M.91-199], x 5.9; 16 - dorsal view of paratype, EF-21.2 [M.91-199], x 5.1; 18 - frontal view of carapace, EF-21.2 [M.91-199], x 5.9.

PLATE 6



MÁFI collected by Magyar Lajos from Kissvábhegy. *Phlyctenodes hantkeni* Lőrenthey, 1897, is the only decapod species of Facies 4 which has not been found during the course of the present research. Because the matrix on Lőrenthey's specimens is not characteristic, they may originate from Facies 5.

Genus *Priabonocarcinus* gen. nov.

*Derivation of name* — From the geological stage name and *-carcinus*.

*Type species* — *Priabonocarcinus gallicus* sp. nov.

*Diagnosis* — Carapace transversely subhexagonal, thin anterolateral margins with two rudimentary spines, the one on the lateral angle weakly ridged; the front narrowly and evenly rounded, orbits small and circular.

***Priabonocarcinus gallicus* sp. nov.**

Pl. 5, Figs 12, 15, 16; text-fig. 4e

*Derivation of name* — From Francia-kőfejtő, meaning 'Quarry of the Frenchman'.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-25.1 [M.91-180]) and paratypes EF-25.2-4 [M.91-180].

*Description* — The carapace is transversely subhexagonal in outline, almost twice as broad as long, nearly flat transversely and moderately arched longitudinally. Small, forwardly directed orbits take up the outer fourths of the orbitofrontal margin which occupies half of the carapace width. The upper orbital margin is thickened by a rounded ridge which tapers towards the front and terminates at a shallow median groove just behind the frontal margin; there is a relatively steep post-orbital depression. The depressed front is narrowly rounded with an inconspicuous median notch. A rudimentary spine occurs a little more than half way along the broadly rounded anterolateral margin and another of about equal size at the lateral angle leads to a weak posteriorly inclined epibranchial ridge. The margin between the spines is straight in juveniles, becoming slightly convex as growth advances. The edge is narrowly rounded and the sides are steeply inclined under. The only surface features are a pair of gastric pits set close to the midline about mid-carapace length; the urogastric lobe is depressed and laterally delimited by epimeral adductor muscle scars. Internal moulds show three small tubercles in an inverted triangle on the lingulate cardiac region.

*Discussion* — There is in the general outline of the carapace, the rudimentary anterolateral spines and

weak epibranchial ridge a considerable likeness to the Middle Eocene genus *Proxicarpilius* Collins & Morris, 1978, and in particular to *Proxicarpilius minor* Collins & Morris, 1978. In *Priabonocarcinus gallicus* sp. nov., however, the orbits are comparatively smaller, the front is regularly convex and notched, rather than convex-concave and entire, and the inner orbital angles are rounded, not angular. The new species shows some similarities to *Atergatis* de Haan, 1833, especially to *Atergatis floridus* (Linné, 1767) in having an almost entire, tapered anterolateral margin and a short ridge extending from the lateral angle, also in having a smooth carapace surface; the development of the front, however, is completely different in being weakly notched and deflected in *Priabonocarcinus* and lobate in *Atergatis*.

Genus *Prochlorodius* gen. nov.

*Derivation of name* — Indicating an early member of the *Chlorodius* Group.

*Type species* — *Prochlorodius ellipticus* sp. nov.

*Diagnosis* — Carapace transversely elliptical with a median dorsal depression, three pairs of anterolateral spines and the orbitofrontal margin exceeds half the carapace width.

***Prochlorodius ellipticus* sp. nov.**

Pl. 5, Fig. 11; Pl. 6, Figs 4, 7, 17; text-figs 4i, j

*pars* 1898b *Neptocarcinus millenaris* Lőrenthey, p. 179, pl. 4 non fig. 3.

*pars* 1898c *Neptocarcinus millenaris* Lőrenthey — Lőrenthey, p. 69, pl. 4, fig. 4 non fig. 3.

*pars* 1929 *Neptocarcinus millenaris* Lőrenthey — Lőrenthey in Lőrenthey & Beurlen, p. 216, pl. 10, fig. 4 non fig. 3.

*Derivation of name* — From the carapace outline.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-20.1 [M.91-181]) and paratypes, carapaces (EF-20.2-16 [M.91-181]; EK-20.1-67 [M.91-182], EGA-13.1-5 [M.91-184], EGF-8.1-5 [M.91-185], ?EK-28.1-5 [M.91-183]).

*Description* — The carapace is transversely elliptical in outline, about one third broader than long, widest about midlength. In side view it rises steeply behind the front to the anterior third, then slopes gently to the posterior margin, it is flatly arched transversely and both sections encompass a moderately deep depression centred about the cervical furrow. The orbitofrontal margin occupies three



fourths of the carapace width; taking up a half of this the front has a shallow median depression and deep notches where the protogastric furrows meet the front. The frontal rim is bounded by a thin ridge behind which a faint median furrow separates obscure frontal lobes. The orbits are broadly ovate, the inner orbital spine is sharp and the outer one rounds into the anterolateral margin which has three more or less even sized spines whose bases are slightly raised onto the dorsal surface. Weakly sinuous posterolateral margins converge to the posterior margin which is about as wide as the front. The regions are poorly defined. The cervical furrow is sinuous medially, turns sharply round the base of the mesogastric lobe then curves broadly to the margin. The dorsal surface is generally smooth, pits crowd the upper orbital margin and a line of pits crosses the front.

*Discussion* — While drawing attention to their much smaller size, Lörenthey (1898b, pl. 4, fig. 4) attributed with reservation two specimens to *Neptocarcinus millenaris*. Small specimens of *Neptocarcinus millenaris*, however, are much flatter than specimens of equal size of *Prochlorodius ellipticus* and the slight similarity in their outline is only superficial. The sharp anterolateral margin of *Neptocarcinus* resembles that of many portunids, *Prochlorodius* has a typical xanthid margin. *Prochlorodius* has much in common with several species now included in *Chlorodiella* Rathbun, 1897. However, the width of the orbitofrontal margin relative to the carapace width is much greater than that of *Chlorodiella* which is 'about a half' according to Serène (1984). *Prochlorodius ellipticus* appears to be close to *Chlorodiella barbata* (Borradaile, 1900), but the latter lacks the dorsal median depression.

We previously considered several small carapaces (EK-28.1-5, Pl. 5, Fig. 11) to belong to *Pilumnus* Leach, 1815, but their orbits and frontal margins, together with the median depression, fully agree with *P. ellipticus*. In the EK-28 specimens, however, the anterolateral margins are subparallel, while converging frontally in *Prochlorodius* — thus presenting a different appearance to the carapace. At the moment it seems safer to regard the smaller EK-28 specimens as juveniles possibly belonging to *P. ellipticus*, explaining differences to allometric growth.

Genus *Syphax* A. Milne Edwards, 1864

*Type species* — *Syphax crassus* A. Milne Edwards, 1864, by original designation. Range: Early Tertiary.

### **Syphax** sp.

Pl. 6, Fig. 3

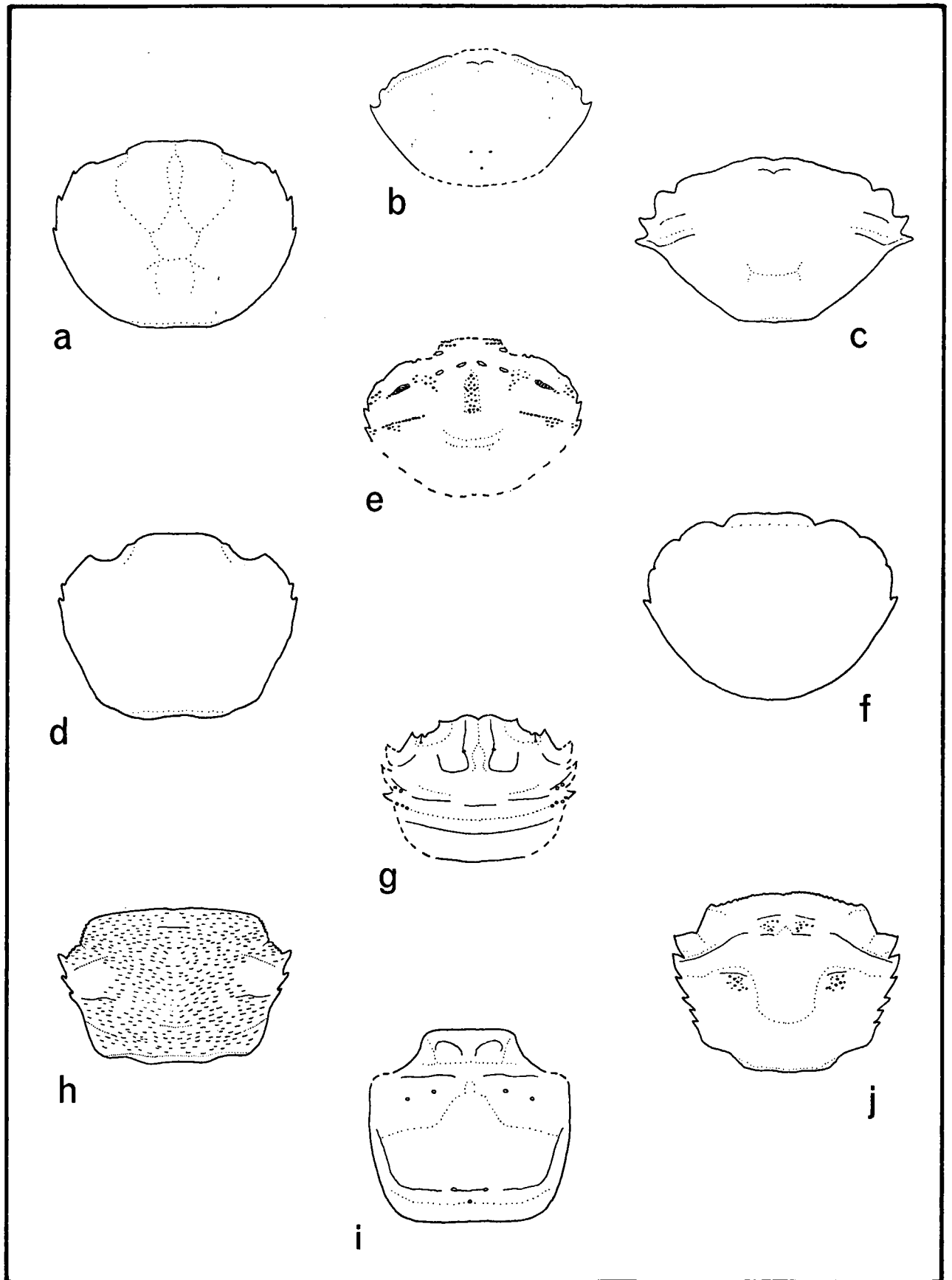
*Material* — A carapace, EK-23.1 [M.91-186].

*Description* — Carapace subpentagonal in outline almost as broad as long, gently arched in transverse and longitudinal sections. The front is divided by a median notch, its nearly straight sides slope gently back to a notch at the inner orbital angle. The orbits are directed obliquely outwards and the upper margin terminates in another notch immediately before a small outer orbital spine. There is an indentation in the margin coincident with the hepatic furrow followed by a spine, the margin is then straight to a spine at the lateral angle. The posterolateral margin is about as long as the combined anterolateral and orbital margins. The cervical furrow is very shallow at the midline, it deepens round the base of a node at each corner of the mesogastric lobe, curves forward and outward round the protogastric lobe and turns sharply out to reach the margin at the lateral angle. The hepatic furrow is as wide as the cervical furrow and partly encloses a C-shaped tubercle on the hepatic regions. Narrow, rectangular frontal lobes are separated from obliquely ovate epigastric lobes, in turn separated from large bilobate protogastric lobes which have a granule anteriorly on each inner, and two on each outer lobe. The very small mesogastric lobe has a tubercle at the basal angles and a median granule; the anterior process is constricted at its base and has a granule apically. The urogastric lobe is damaged, but appears as a narrow crescent. The lateral portion of the branchiocardiac furrow bounds a group of three fused granules forming the mesobranchial lobe and the epibranchial is quadrate.

*Discussion* — While agreeing, by and large, with Milne Edwards's figure of *Syphax crassus* (see Glaessner, 1969) *Syphax* sp. differs in having a curved node on the hepatic regions, a smaller mesobranchial lobe — triangular in outline rather than rectangular — and more deeply divided protogastric lobes.

Genus *Titanocarcinus* A. Milne Edwards, 1864

*Type species* — *Titanocarcinus serratifrons* A. Milne Edwards, 1863, by subsequent designation of Glaessner (1929). Range: Late Cretaceous-Miocene.



**Titanocarcinus kochii** Lőrenthey, 1897

Pl. 6, Figs 2, 5, 6

- 1897 *Titanocarcinus kochii* Lőrenthey, p. 155.  
 1929 *Laevicarcinus kochi* (Lőrenthey) — Lőrenthey & Beurlen,  
 p. 239, pl. 11, figs 4, 5.  
 1969 *Titanocarcinus kochii* Lőrenthey — Via, p. 420 (with  
 synonymy).

*Material* — The type series is in the collection of MÁFI. New material: EF-27.1-5 [M.91-187], EK-27.1 [M.91-188], EGF-11.1 [M.91-189].

*Remarks* — The inhomogeneity of *Titanocarcinus* calls for a severe revision of the genus. Neogene species seem to have been eliminated and even Palaeogene ones are quite heterogenous as emphasised by Busilini *et al.* (1984). Nevertheless, *T. kochii* should be preserved in the framework of this genus until a revision and disassociation from *Laevicarcinus* (see above), which is a completely different, probably *Panopeus*-related form, is undertaken.

Genus *Eomaldivia* gen. nov.

*Derivation of name* — Indicating an early *Maldivia*.

*Type species* — *Eomaldivia pannonica* sp. nov.

*Diagnosis* — Carapace subhexagonal with two or three pairs of lateral spines; the front occupies two thirds or more of the carapace width and is interrupted by a median notch.

*Remarks* — In all probability the species, and consequently the genus, is related to *Trapezia* (*i.e.* to the family Trapeziidae as recognised by Serène, 1984). Similar smooth, featureless carapaces are present only in this group. The strong anterolateral spines in *Eomaldivia* suggests a close relationship to *Maldivia* although its much wider front relates it rather to *Tetralia* or *Trapezia*. All related forms are obligate commensals with scleractinians or octocorals.

**Eomaldivia pannonica** sp. nov.

Pl. 6, Figs 10, 13; text-fig. 4k

*Derivation of name* — From Pannonia, the Roman province incorporating part of present-day Hungary.

Fig. 5. Diagrammatic views of: a - *Branchioplax sulcata* sp. nov., b - *Corallicarcinus planus* gen. et sp. nov., c - *Corallicarcinus spinosus* (Lőrenthey), d - *Eoplax minima* gen. et sp. nov., e - *Caprocancer altus* gen. et sp. nov., f - *Lobogalenopsis quadri-lobata* (Lőrenthey), g - *Sculptoplax rigida* gen. et sp. nov., h - *Daragrapsus trispinosus* gen. et sp. nov., i - *Palaeograpsus bittneri* sp. nov., j - *Daranyia granulata* Lőrenthey.

*Diagnosis* — An *Eomaldivia* with two pairs of lateral spines, the front occupies rather more than two thirds of the carapace width.

*Material* — Holotype, a carapace (EGA-12.1 [M.91-190]) and paratypes EGA-12.2-4 [M.91-190].

*Description* — The carapace is subhexagonal in outline, about one fifth wider than long and widest between the 2nd and 3rd lateral spines a little more than half the distance from the front; transversely and longitudinally moderately arched. The anterolateral margins are parallel and sinuous posterolateral margins converge sharply to acutely rounded posterior angles. The posterior margin is about half the width of the front and bounded by a groove extending almost to the lateral angle. The broadly rounded orbitofrontal margin occupies almost the entire carapace width, of this the front takes up more than two thirds and protrudes slightly beyond acute inner orbital spines. A fine ridge lines the upper orbital margin and extends across the front. A sharp outer orbital spine points obliquely outwards in line with the shallow orbit, its outer edge leads directly to a concavity forming the fore-edge of the first lateral spine which is sharp, more forwardly directed, and its outer edge, again, leads to a concave fore-edged needle-sharp spine at the lateral angle. Surface features are limited to a depression behind the orbits with a weaker, more medial one behind it. The triangular mesogastric lobe is weakly tumid at its outer angles and a shallow depression outlines the urogastric and cardiac regions. The lateral areas of the dorsal surface are lightly pitted.

**Eomaldivia trispinosa** sp. nov.

Pl. 6, Figs 8, 11; text-fig. 4l

*Derivation of name* — Alluding to the three pairs of anterolateral spines.

*Diagnosis* — An *Eomaldivia* with three pairs of anterolateral spines.

*Material* — Holotype, a carapace (EF-19.1 [M.91-191]), and paratypes EF-19.2-4 [M.91-191], EBA-14.1-2 [M.91-192].

*Description* — The carapace is similar in outline to *Eomaldivia pannonica*, but a little longer in relation to width, the front is narrower and the lateral angles are situated a little more posteriorly. The anterolateral margins are slightly convex and have three pairs of spines, the 1st coming immediately behind a small outer orbital spine. On the dorsal surface the

postorbital depressions are shallower and more continuous round the upper orbital margins, they have no other depression posterior to them. On the whole the median regions are less well defined, although the metabranchial lobes are vaguely tumid. There is a pair of gastric pits level with the lateral angles.

Genus *Tetralia* Dana, 1851

*Type species* — *Tetralia nigrifrons* Dana, 1853 (= *Cancer glaberrimus* Herbst, 1790), ICZN Code 69a (v). *Tetralia nigrifrons* is now the type species of *Tetraloides* Galil, 1985, but the designation of *C. glaberrimus* still stands. Range: Late Eocene-Recent.

***Tetralia loerentheyi* (Müller, 1975)**

Pl. 6, Figs 9, 12, 15; text-fig. 4m

1975 *Trapezia loerentheyi* Müller, pp. 516, 520, pl. 1, fig. 1.

*New material* — Carapaces (EK-1.1-6 [M.91-194], EF-18.1-15 [M.91-193], EGA-22.1-4 [M.91-197], EGF-7.1-5 [M.91-198], EBA-15.1-5 [M.91-195], EBV-6.1-3 [M.91-196]).

*Remarks* — Newly collected specimens reveal a typically *Tetralia*-like frontal margin absent in the type specimens, consequently the species should be transferred to *Tetralia* although there are two anterolateral spines in the Eocene form. In juvenile *T. glaberrima* only one small lateral spine is visible (see Sakai, 1976, pl. 183) which disappears as growth advances.

Family Goneplacidae MacLeay, 1838  
Subfamily Carcinoplacinae Miers, 1886  
Genus *Branchioplax* Rathbun, 1916

*Type species* — *Branchioplax washingtoniana* Rathbun, 1916, by monotypy. Range: Eocene-Oligocene.

***Branchioplax sulcata* sp. nov.**

Pl. 6, Figs 14, 16, 18; text-fig. 5a

1898b ?*Plagiolophus* Lörenthey, p. 195.  
1898c ?*Plagiolophus* Lörenthey — Lörenthey, p. 73.  
1975 *Branchioplax?* sp. — Müller, pp. 516, 520.

*Derivation of name* — Alluding to the conspicuous sulcae.

*Diagnosis* — A *Branchioplax* with conspicuous furrows.

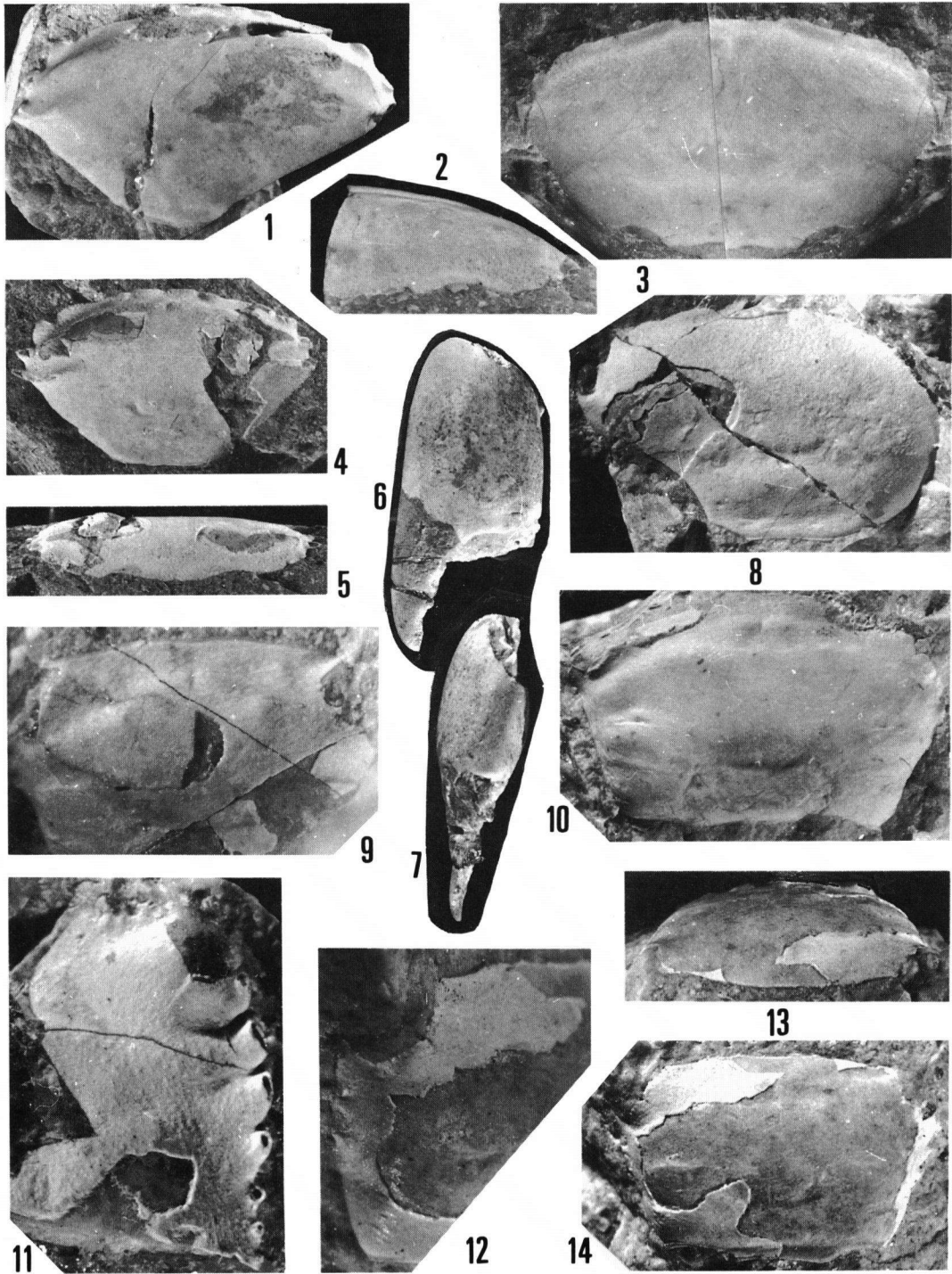
*Material* — Holotype, a carapace (EF-21.1 [M.91-199]) and paratypes, a carapace fragment on a piece of rock with a carapace of '*Palaeograpsus* sp.' from Kissvábhegy, coll. MÁFI and EF-21.2-8 [M.91-199], EK-21.1-7 [M.91-200], EBM-6.1 [M.91-202], EBA-16.1-8 [M.91-201], EBV-5.1-2 [M.91-203], ?EGA-22.1-4.

*Description* — The carapace is subquadrate in outline, almost as long as wide, widest at its anterior third; gently arched longitudinally and transversely. There are two blunt spines on the rather short anterolateral margins and another, smaller one, just behind the cervical notch. Rounded posterolateral margins curve smoothly into the straight to slightly concave posterior margin which is bounded by a flattened ridge with a granule at either end. The orbitofrontal margin is straight to slightly convex and occupies about seven tenths of the carapace width. Small rounded orbits take up the outer fourths and are directed a little obliquely from the midline. The almost straight front is produced, thickened, with a shallow median depression. The inner orbital angles are rounded, there are two

PLATE 7

- Figs 1, 4, 5 *Coralliocarcinus spinosus* (Lörenthey), 1 - dorsal view of carapace, EK-25.2 [M.91-205], x 2.2; 4 - dorsal view of carapace, EK-25.1 [M.91-205], x 2.3; 5 - frontal view of carapace, EK-25.1 [M.91-205], x 2.3.
- Figs 2, 3, 8 *Coralliocarcinus planus* gen. et sp. nov., 2 - frontal view of carapace, holotype, EK-26.1 [M.91-207], x 5.4; 3 - dorsal view of carapace, montage of left side, EK-26.1 [M.91-207], x 5.4; 8 - dorsal view of carapace, paratype, EK-26.2 [M.91-207], x 3.7.
- Figs 6, 7 ? *Coralliocarcinus spinosus* (Lörenthey), outer and upper views of right propodus, EK-25.11 [M.91-205], x c. 2.
- Figs 9, 10, 12-14 *Daragrapsus trispinosus* gen. et sp. nov., 9 - dorsal view of carapace, paratype, EK-30.1 [M.91-209], x 8.7; 10 - dorsal view of carapace, paratype, EF-30.2 [M.91-208], x 3.6; 12 - dorsal view of carapace, disoriented to show orbit and spines on the left side, holotype, EK-30.1 [M.91-209], x 7.2; 13 - frontal view of carapace, EK-30.1 [M.91-209], x 4.6; 14 - dorsal view of carapace, EK-30.1 [M.91-209], x 4.6.
- Fig. 11 *Daranyia granulata* Lörenthey, dorsal view of carapace showing right orbit and lateral spines, EF-29.2 [M.91-215], x 6.6.

PLATE 7



obscure fissures in the raised upper margin and the outer orbital spine is only weakly developed. Where it crosses the midline the cervical furrow is broadly V-shaped and vague to its junction with the proto/hepatic furrows extending from the anterior angle of the mesogastric lobe to about the middle of the orbital margins; they are by far the most prominent dorsal features. The short urogastric lobe is depressed and its outer angles are attenuated; it is confluent with the somewhat tumid rounded-triangular cardiac region which has three granules in an inverted triangle. Between the urogastric and the cardiac region is a small node just isolated from a ridge bounding the course of an otherwise obsolete branchiocardiac furrow. The weakly defined very slender anterior process of the mesogastric lobe does not quite reach the anterior border of the protogastric lobes. There is an obscure granule at the anterior centre of the epigastric lobes and a larger one in the middle of each protogastric lobe.

*Discussion* — *Branchioplax sulcata* closely resembles *Branchioplax concinna* Quayle & Collins, 1981 from the Barton Clay of Christchurch (England), but differs in having more prominent proto-hepatic furrows and a somewhat less produced frontal margin. (Better preserved specimens of *Branchioplax concinna* have a much less obvious frontal 'notch' than the description in Quayle & Collins [1981] implies). The urogastric lobe of the new species is quadrate rather than rectangular as in *Branchioplax concinna*. Furrows of more or less even depth and width, together with a sparse median ornament of granules and absence of granules on the epi- and protogastric lobes readily distinguishes *Branchioplax washingtoniana* (Eocene/Oligocene of North America) from *B. sulcata*.

Genus *Caprocancer* gen. nov.

*Derivation of name* — The Latinised form of Kecske (a goat) and the suffix *-cancer*.

*Type species* — *Caprocancer altus* sp. nov.

*Diagnosis* — Carapace subpentagonal with three marginal spines; it is steeply arched in transverse and longitudinal sections; granulated ridges form a curve across the front and there is a similar ridge on the epibranchial lobes.

***Caprocancer altus* sp. nov.**

Pl. 8, Figs 1-3; text-fig. 5e

*Derivation of name* — From the steeply arched longitudinal and transverse sections.

*Diagnosis* — As for genus.

*Material* — Holotype, a fragmentary carapace (EK-31.1 [M.91-204]), paratypes, EK-31.2-4 [M.91-204].

*Description* — The carapace is subpentagonal in outline, widest a little anterior to midlength. In longitudinal section it rises steeply from the front, reaches maximum height in the anterior fifth, becomes depressed at the base of the anterior mesogastric process, then curves gently to the posterior margin; it is steeply arched transversely. Only a corner of the forwardly facing orbits and a small outer orbital spine is preserved. The anterolateral margin is convex to a slight indentation where the protogastric groove meets the edge, behind this a basal scar indicates a small upturned spine, the margin then extends almost straight to a triangular spine, also upturned, and this is followed by a smaller spine more laterally directed. Concave posterolateral margins are at least as long as the anterolateral margins and converge to a posterior margin narrower than the front. The cervical furrow crosses the midline posterior to mid-length, curves sharply round the mesogastric lobe and becomes obsolete as it passes round a curved granulated ridge on the epibranchial lobe. The inner end of this ridge is a little anterior to the pentagonal mesogastric lobe. A shorter, steeper ridge on the hepatic region, together with a pair of nodes on either side of the anterior mesogastric process forms an illusory curve across the front. The deepest grooves are those delineating the anterior mesogastric process which is parallel sided for most of its length and terminates some distance from the front. The urogastric lobe is crescent shaped and narrower than the mesogastric lobe. Numerous granules of several diameters crowd the dorsal surface.

Genus *Corallicarcinus* gen. nov.

*Derivation of name* — With reference to the coral-associated habitat.

*Type species* — *Corallicarcinus spinosus* (Lőrenthey, 1929).

*Diagnosis* — Carapace subhexagonal with three pairs of anterolateral spines, front straight and bilobed; ridges extend onto the dorsal surface from the 2nd and 3rd marginal spines.

***Corallicarcinus spinosus* (Lőrenthey, 1929)**

Pl. 7, Figs 1, 4-7; text-fig. 5c

1929 *Neptocarcinus spinosus* Lőrenthey, p. 217, pl. 10, fig. 5.

1929 *Galenopsis similis* Bittner — Lőrenthey & Beurlen, p. 247, pl. 16, fig. 7.

*Diagnosis* — The front occupies less than one third of the orbital margin, the anterolateral spines are robust and the dorsal ridges are strongly developed.

*Material* — Holotype, a carapace, housed in MAFI Coll. Additional material: carapaces EK-25.1-27 [M.91-205], EGA-18.1-9 [M.91-206].

*Description* — The carapace is broadly subhexagonal with the front and anterolateral margins forming an almost continuous curve; in longitudinal section it rises steeply behind a narrow flat frontal area, curves sharply to its highest point level with the 2nd lateral spines, then gently to the posterior margin, it is weakly arched transversely. The orbitofrontal margin takes up almost two thirds of the carapace width and of this the front occupies rather more than one third; it is broadly bilobed and slightly in advance of a bluntly rounded inner orbital spine from which it is separated by a notch, the upper orbital margin is slightly raised. Deep notches separate the outer orbital and slightly upturned anterolateral spines; the first is robust, subtriangular with a rounded posterior edge, the 2nd, about half the size is rounded in section, and the 3rd is almost spinulate. A broadly rounded ridge from the 2nd spine extends almost to the midline where it is interrupted by the narrow anterior mesogastric process; a sharper ridge from the 3rd spine forms the epi-branchial lobe. The posterior angles are fairly sharp and the posterior margin is about as wide as the front. Internal moulds show an ovate mesogastric lobe with two pairs of small granules, and the epigastric lobes are vaguely tumid. The slightly depressed confluent uro-cardiac region is subtriangular and broader than the mesogastric lobe.

A propodus attributed to this species (Pl. 7, Figs 6, 7) is robust and ovate in section; the height of the manus rather exceeds twice the length, its upper margin is weakly convex, the lower margin is convex proximally and almost straight distally to half the length of the fixed finger which is less than half the length of the manus and its opposing margin has a row of uneven granules apart from an excavation behind the tip.

***Corallicarcinus planus* sp. nov.**

Pl. 7, Figs 2, 3, 8; text-fig. 5b

*Derivation of name* — With reference to the subdued surface feature.

*Diagnosis* — Anterolateral spines and dorsal ridges weakly developed and the front occupies about half of the orbitofrontal margin.

*Material* — Holotype, a carapace (EK-26.1 [M.91-207]) and paratypes, EK-26.2-6 [M.91-207].

*Description* — In longitudinal section the carapace is steeply downturned in front, transversely it is nearly flat. The anterolateral spines are weakly developed, with the stoutest at the lateral angle. The front takes up a little under a half of the orbitofrontal margin, it is straight with a shallow median notch and not much advanced from the inner orbital spine. The ridges extending from the 2nd and 3rd lateral spines are feebly developed, there is a sinuous depression at the urogastric/cardiac junction and a small wedge-like pit next to the outer angles of the mesogastric lobe.

*Discussion* — The presence of dorsal ridges distinguishes *Corallicarcinus* from *Neptocarcinus*. These ridges are more strongly developed in *C. spinosus*, which also differs from *C. planus* in having more robust lateral spines and a narrower front in proportion to the orbitofrontal margin.

Genus *Eoplax* gen. nov.

*Derivation of name* — From the Eocene and the suffix *-plax* (flat) used in the names of many related genera.

*Type species* — *Eoplax minima* sp. nov.

*Diagnosis* — Carapace subhexagonal with two pairs of lateral spines, the posterior pair vestigial; front not much produced, inner orbital angle rounded; regions poorly defined. Dorsal surface with wavy grapsoid ornament.

***Eoplax minima* sp. nov.**

Pl. 8, Figs 6, 7; text-fig. 5d

*Derivation of name* — Indicating the small size of the species.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EF-28.1 [M.91-219]) and paratypes, EBA-21.1-2 [M.91-220].

*Description* — The carapace is subhexagonal in outline, the length about five sixths of the breadth, broadest at the anterior third. There is a small forwardly directed spine at the lateral angle and a vestigial one behind it. The short anterolateral margin is straight before the lateral angle, angularly bent, then straight to where a post-orbital depression causes a notch at the margin. The front is barely produced, convex-concave and curves into the inner orbital angle; it takes up half of the orbitofrontal margin which occupies two thirds of the

carapace width. Circular orbits are directed slightly obliquely to the midline. Straight posterolateral margins converge to shallow coxigeal embayments before sharply rounded posterior angles and the posterior margin is wider than the front. The cervical furrow is straight and moderately deep where it crosses the midline some three fourths distant from the front. Surface features are limited to a pair of narrow steep-fronted epigastric lobes leading back as truncated triangles onto the protogastric lobe. Traces remain on the external mould of the fine wavy-ridged typically grapsoid ornament.

*Discussion* — There is considerable likeness to the Badenian (Middle Miocene) *Pachygrapsus hungaricus* Müller, 1974, but the latter species has a more quadrate outline, the marginal spines are more strongly developed and there is an outer orbital spine, the epigastric lobes are quadrate rather than 'triangular'. Strong outer orbital spines and a varying number of lateral spines are features of Recent grapsids.

Genus *Galenopsis* A. Milne Edwards, 1865

*Type species* — *Galenopsis typica* A. Milne Edwards, 1865, by subsequent designation of Glaessner (1929). Range: Middle Eocene-Pliocene.

***Galenopsis similis* Bittner, 1875**

Pl. 8, Figs 4, 5

- 1875 *Galenopsis similis* Bittner, p. 97, pl. 2, fig. 9.  
1929 *Galenopsis similis* Bittner — Lörenthey & Beurlen, p. 247, pl. 16, figs 3, 4, 6 non 7 (see also for synonymy).  
1969 *Galenopsis similis* Bittner — Via, p. 378.  
1975 *Galenopsis* aff. *similis* Bittner — Müller, pp. 510, 516.

*Additional material* — 3 carapaces, 3 chelae (EK-24.1-6), 19 carapaces (EGA-23.1 [M.91-225], EF-36.1-12 [M.91-221], EBK-7.1-2 [M.91-223], EBV-9.1-4 [M.91-224], EK-37.1 [M.91-222]).

*Description* — The length of the subpentagonal carapace is about four fifths of the width, widest at its anterior third. In side view it is steeply arched over the anterior third and gently curved to the posterior margin; it is moderately arched transversely. The anterolateral margin (spinose in very young individuals) is divided by two evenly spaced lobes before a small, sharp spine at the lateral angle. A brief dorsal depression before the spine gives emphasis to a low epibranchial 'ridge'. Straight posterolateral margins converge and lead by way of shallow coxigeal depressions to the gently convex posterior margin which is about as wide as the front. The orbitofrontal margin occupies half of the carapace width and the almost circular orbits take up the outer fourths. There is a weak median depression in the slightly protruding front and a deep concavity before a blunt inner orbital spine; the upper margin is weakly raised and the outer angle is sharp. A narrow postfrontal depression commencing at the outer orbital spine broadens towards the front. The cervical furrow is broadly V-shaped from a pair of gastric pits close to the midline two thirds distant from the front, its forward and outward curve to the margin is marked by a series of pits. The tip of the anterior mesogastric process extends between vaguely tumid epigastric lobes. Numerous coarse pits isolate the cardiac region on which are three obscure granules. Other, finer pits crowd the dorsal surface.

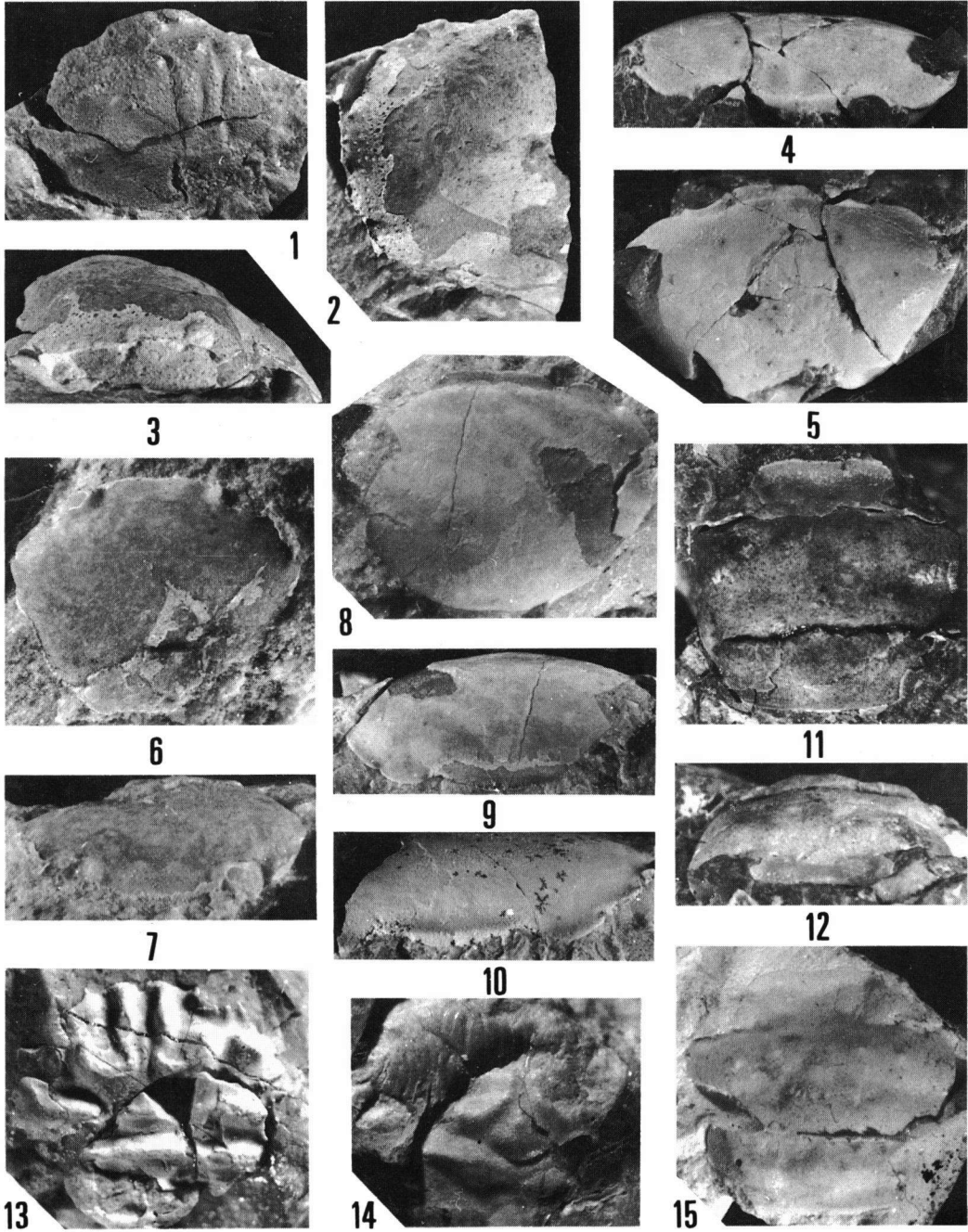
The undersurface and limbs were figured by Lörenthey (1929, pl. 16, fig. 4).

PLATE 8

- Figs 1-3 *Caprocancer altus* gen. et sp. nov., 1 - dorsal view of carapace, holotype, EK-31.1 [M.91-204], x 2; 2 - frontal view of carapace, paratype, EK-31.2 [M.91-204], x 1.8; 3 - left lateral view of carapace, EK-31.2 [M.91-204], x 1.8.  
Figs 4, 5 *Galenopsis similis* Bittner, 4 - frontal view of carapace, EF-36.1 [M.91-221], x 3.8; 5 - dorsal view of carapace, EF-36.1 [M.91-221], x 3.8.  
Figs 6, 7 *Eoplax minima* gen. et sp. nov., 6 - dorsal view of carapace, holotype, EF-28.1 [M.91-219], x 7.2; 7 - frontal view of carapace, EF-28.1 [M.91-219], x 7.2.  
Figs 8-10 *Lobogalenopsis quadrilobata* (Lörenthey), 8 - dorsal view of carapace, EK-33.8 [M.91-226], x 3; 9 - frontal view of carapace, EK-33.8 [M.91-226], x 3; 10 - frontal view of carapace, EK-33.2 [M.91-226], x 1.8.  
Figs 11, 12, 15 *Palaeograpsus bittneri* sp. nov., 11 - dorsal view of internal mould of carapace, holotype, EF-31.1 [M.91-227], x 8.9; 12 - frontal view of internal mould of carapace, EF-31.1 [M.91-227], x 8.9; 15 - dorsal view of latex of carapace, EF-31.1 [M.91-227], x 8.9.  
Fig. 13 *Sculptoplax rigida* gen. et sp. nov., dorsal view of carapace, holotype, EK-32.1 [M.91-228], x 5.3.  
Fig. 14 *Costacopluma* ? sp., dorsal view of carapace, partly overlain by *Galathea* sp., EK-34.1 [M.91-229], x 5.5.



PLATE 8



*Discussion* — The figure presented in Lórenthey & Beurlen (1929, pl. 16, fig. 7) omits the the concavities in the frontal margin, places the lateral extremities of the postfrontal depression much too far posteriorly (reaching the 2nd anterolateral lobes), extends the epibranchial ‘ridge’ and altogether over-emphasises the mesogastric and cardiac regions. These characters agree entirely with *Corallicarcinus spinosus* (Lórenthey) and the specimen should be regarded as belonging to that species.

Genus *Lobogalenopsis* gen. nov.

*Derivation of name* — *Lobo-* for the lobate anterolateral margins and *Galenopsis*.

*Type species* — *Galenopsis quadrilobata* Lórenthey, 1897.

*Diagnosis* — Carapace strongly convex; elliptical with a sharply keeled, lobate anterolateral margin; very small orbits and a deflected, broadly triangular frontal margin, straight in upper view.

### **Lobogalenopsis quadrilobata**

(Lórenthey, 1897)

Pl. 8, Figs 8-10; text-fig. 5f

- 1897 *Galenopsis quadrilobatus* Lórenthey, p. 156.  
1898a *Galenopsis quadrilobatus* Lórenthey — Lórenthey, p. 100.  
1898b *Galenopsis quadrilobatus* Lórenthey — Lórenthey, p. 87, pl. 5, fig. 3.  
1898c *Galenopsis quadrilobatus* Lórenthey — Lórenthey, p. 60, pl. 5, fig. 3.  
1929 *Galenopsis quadrilobatus* Lórenthey — Lórenthey & Beurlen, p. 249, pl. 16, fig. 5.  
1933 *Galenopsis quadrilobatus* Lórenthey — di Salvo, pl. 33, pl. 3, fig. 3.  
1969 *Galenopsis quadrilobatus* Lórenthey — Via, p. 378.

*Material* — The type series is housed in MAFI. Additional material: EK-33.1-8 [M.91-226].

*Remarks* — Although placed by Lórenthey in *Galenopsis*, *Lobogalenopsis quadrilobata* is similar to that genus only in the broad outline of its carapace. Its extremely small orbital sinus - in fact only a notch-like space between the frontal margin and the 1st anterolateral spine - readily distinguishes it from *Galenopsis* which has well-developed orbits. The front of *Lobogalenopsis*, straight in upper view, differs also from the lobate one of *Galenopsis*. It would be difficult to define affinities for the new genus; its outline and convexity relates it to *Pilumnus*, but the orbits and front differ considerably.

Family Grapsidae Macleay, 1838

Genus *Daragrapsus* gen. nov.

*Derivation of name* — While related to *Daranyia*, there are similarities to *Grapsus*-related forms.

*Diagnosis* — Carapace subquadrangular, lateral margins with three spines decreasing in size posteriorly; frontal median furrow not continued onto the mesogastric lobe.

*Type species* — *Daragrapsus trispinosus* sp. nov.

### **Daragrapsus trispinosus** sp. nov.

Pl. 7, Figs 9, 10, 12-14; text-fig. 5h

*Derivation of name* — From the three pairs of lateral spines.

*Diagnosis* — As for genus.

*Material* — Holotype, a carapace (EK-30.1 [M.91-209]) and paratypes, EK-30.2-21 [M.91-209], EF-30.1-21 [M.91-208], EGA-17.1-10 [M.91-213], EGF-14.1-13 [M.91-214], EBA-19.1-4 [M.91-210], EBK-8.1 [M.91-211], EBV-10.1-3 [M.91-212].

*Description* — The subquadrate carapace is about three fourths wider than long, widest at the outer orbital angles; viewed from the side it rises steeply from the front then becomes moderately curved to the posterior margin, in transverse section it is gently arched with steep sides. The lateral margins are straight and converge to embayments for the fifth coxae set more or less in line with the posterior margin which is bounded by a fine ridge followed by a groove more prominent medially. The orbitofrontal margin is not well preserved, the front appears to be nearly straight or broadly rounded, it leads without interruption to straight, gently sloping upper orbital margins terminating in strong, flat, forwardly directed hooked spines. Three similarly shaped lateral spines diminish in size posteriorly; the 1st and 2nd occur on the hepatic margin and the 3rd behind the cervical furrow. A fine median groove separates small ovate epigastric lobes and divides to enclose the tip of a poorly defined anterior mesogastric process. The cervical furrow curves broadly round the base of the mesogastric lobe and turns abruptly forward before curving out to the lateral margin; three regularly spaced pit-like depressions line its base. Vague ridges extend from the epigastric lobes towards the outer orbital spines; a similar ridge between a granule on each proto-gastric lobe becomes prominent and downturned towards the margins; a ridge bounds the cervical and another the concave branchiocardiac furrow. The confluent uro-cardiac region is broadly shield-shaped and has one median granule and a pair of

ridged granules at its base. A pair of elongate granules on the mesogastric lobe lies close to the midline and is followed by two or three pairs of rugose granules lining the lateral and basal margins. The entire dorsal surface is granulated, the granules tending to form short, alternating ridges.

*Discussion* — While closely related to the contemporary genus *Daranyia* Lórenthey, 1901, *Daragrapsus* differs in having only three pairs of lateral spines; the anterior border of the protogastric lobes has two, not four nodes, the frontal median sulcus extends only to the tip of the anterior mesogastric process, not continuing the length of the mesogastric lobe as it does in *Daranyia* and the transverse furrows on the latter genus are straighter.

Genus *Daranyia* Lórenthey, 1901

*Type species* — *Daranyia granulata* Lórenthey, 1901, by monotypy. Range: Late Eocene.

***Daranyia granulata* Lórenthey, 1901**

Pl. 7, Fig. 11; text-fig. 5j

- 1901a *Daranyia granulata* Lórenthey, p. 334, pl. 1, fig. 3.  
 1902 *Daranyia granulata* Lórenthey, p. 33.  
 1908 *Daranyia granulata* Lórenthey — Lórenthey, p. 34, pl. 1, fig. 3.  
 1927 *Daranyia granulata* Lórenthey — Lórenthey & Beurlen, p. 251, pl. 16, fig. 11.  
 1969 *Daranyia granulata* Lórenthey — Glaessner, p. R529, fig. 337/5.

*Material* — Lectotype, a carapace (MÁFI E298) and new material: EF-29.1-4 [M.91-215], EK-29.1-7 [M.91-216], EGF-13.1 [M.91-218], EBM-7.1 [M.91-217].

*Remarks* — The description and figure (Lórenthey, 1929; Glaessner, 1969) depicts this species with a weakly bilobed front and massive forwardly directed 'supraorbital' spines; recently collected specimens, however, prove this not to be the case. The front as now known occupies five sixths of the carapace width and is entire, the median third being weakly convex, the outer thirds concave, terminating in a sharp, inner orbital spine; it is lined with spiny granules which are small and crowded medially becoming larger and wider apart laterally. Wide, circular orbits are directed at almost 50° to the midline and the thin upper orbital margin has a long shallow notch immediately alongside the base of a narrow, flattened supraorbital spine next to which is a small outer orbital spine. Then follow the six lateral spines diminishing in size posteriorly as

seen in Lórenthey's (1929) figure. The area behind the orbit — Lórenthey's supraorbital spine-base — is tumid and the median frontal groove does not bisect the front; but terminates behind it.

Genus *Palaeograpsus* Bittner, 1875

*Type species* — *Palaeograpsus inflatus* Bittner, 1875.  
 Range: Middle Eocene-?Oligocene.

***Palaeograpsus bittneri* sp. nov.**

Pl. 8, Figs 11, 12, 15; text-fig. 5i

*Derivation of name* — After Professor A. Bittner.

*Diagnosis* — Carapace subquadrate with no marginal spines, orbits obliquely inclined and a ridge extending across the metabranchial lobes and cardiac region.

*Material* — Holotype, a carapace (EF-31.1 [M.91-227]).

*Description* — The subquadrate carapace is almost flat in transverse section with the sides turned down almost at right angles to the dorsal surface; in side view it is sharply downturned behind the front, flat to a cardiac/metabranchial ridge, then steeply curved to the posterior margin. The orbitofrontal margin occupies three fourths of the carapace width and the orbits are directed almost laterally. A slightly upturned upper orbital margin flattens into a wide rim across a slightly concave front. The anterolateral margins form an abrupt shoulder to the orbits and the lateral margins converge slightly to acute posterior angles. A narrow rim bounds the posterior margin which is a little wider than the front. The cervical furrow is marked by a line of pits where it crosses the midline some two thirds distant from the front, it broadens and deepens as it curves sharply outwards to the margin. Tumid, ovate epigastric lobes are in line with the orbits. The tip of the parallel-sided anterior mesogastric process extends round the edge of the frontal elevation; the triangular mesogastric lobe is more or less confluent with a quadrate urogastric lobe. The extremities of the epimeral adductor muscle scars are marked by pits. A steep round-topped ridge across the subpentagonal cardiac region and metabranchial lobes is heightened by two tubercles on the cardiac region. There is a tubercle on the weakly defined hepatic regions and these, with one on each protogastric lobe, form a curve behind the front; a median tubercle occurs shortly behind them and another, minute, behind the hepatic ones. Very fine granules crowd

the hepatic lobe and coarser ones cover the ‘shoulder’ areas of the protogastric lobes.

*Discussion* — The smaller size, flatter transverse section and wider front immediately distinguishes *Palaeograpsus bittneri* from *Palaeograpsus loczyanus* Lőrenthey, 1897 recorded from Facies 5 of the Szépvölgy Formation; the wider front also distinguishes it from *Palaeograpsus bartonensis* Quayle & Collins, 1981 and *Palaeograpsus depressus* Quayle & Collins, 1981 from the Bartonian of England. *Palaeograpsus guerini* Via, 1969 (Middle Lutetian, Spain) is similar in outline, but the front has a short median sulcus and is less produced; also, the cervical furrow is more pronounced.

Genus *Sculptoplax* gen. nov.

*Derivation of name* — With reference to the strongly sculptured dorsal surface.

*Type species* — *Sculptoplax rigida* sp. nov.

*Diagnosis* — Regions are strongly demarcated by ridges.

***Sculptoplax rigida* sp. nov.**

Pl. 8, Fig. 13; text-fig. 5g

*Derivation of name* — With reference to the strongly ridged dorsal surface.

*Diagnosis* — As for genus.

*Material* — Holotype, a fragmentary carapace (EK-32.1 [M.91-228]) and paratype EK-32.2 [M.91-228].

*Description* — Only the median portion of the carapace remains; it was probably subovate in outline, somewhat broader than long. There is a deep U-shaped notch in the strongly bilobed front which is a little in advance of sharp inner orbital spines. The orbits are directed a little obliquely to the midline and their upper margin is thin, upturned and pierced by two fissures. An oblique ridge surmounts nodose hepatic regions. The base of the triangular mesogastric lobe is transversely ridged and its narrow anterior process extends midway between ridges running back from the frontal margin. These ridges are constricted before recurving onto the protogastric lobes. Epi- and mesobranchial ridges are almost parallel and the mesobranchial lobe is in line with a wide ridged urogastric lobe. The cardiac region is depressed anteriorly and appears to have been broadly rounded. There is a pair of gastric pits at the base of the mesogastric lobe and granules line the hepatic and protogastric ridges.

*Discussion* — There does not appear to be any comparable species described in the fossil record. Several of

the characters described above are shared by xanthids generally, but divided protogastric lobes and transverse ridges are well developed in *Carpilodes* A. Milne Edwards, 1865. The similarity is particularly striking in *Carpilodes supernodosus* Rathbun, 1903, but here the hepatic regions are transverse and larger and there is a median sigmoid extension to the epibranchial lobe; the corresponding area is damaged in *S. rigida*.

Superfamily Ocyphodoidea Rafinesque, 1815  
 Family Retroplumidae Gill, 1894  
 Genus *Costacopluma* Collins & Morris, 1975

*Type species* — *Costacopluma concava* Collins & Morris, 1975, by original designation. Range: Late Cretaceous-Eocene.

***Costacopluma* ? sp.**

Pl. 8, Fig. 14

*Material* — A fragmentary carapace and external mould (EK-34.1 [M.91-229]).

*Description* — Only the median parts of the carapace are preserved; the surface is characterised by strong, sharp transverse ridges, of which a pair of U-shaped ones occur on the protogastric lobes; a second ridge is straight on the branchial regions and slightly V-shaped on the cardiac region, a third ridge running subparallel to the second is anteriorly directed in its median part. There is a longitudinal ridge on the mesogastric lobe. The dorsal surface is smooth.

*Discussion* — The species may well belong to the Retroplumidae, being similar to *Costacopluma* and to some extent to *Retropluma* Gill, 1894. There is some difference, however, in the arrangement of the ridges in the present specimen.

**DISCUSSION**

The fauna of the coral-bearing layer (Facies 4) of the Szépvölgy Limestone is very characteristic because, in all probability, it does not share any species with the overlying, practically coeval Discocylinid Limestone (Facies 5). The typical decapod assemblage of the latter facies consists of raninids, *Calappilia*, *Micromaia*, *Periacanthus*, *Phrynosolambus* etc., which, with the exception of *Micromaia*, are absent from Facies 4. Thus, most of the species dealt with herein may be regarded as truly coral-associated, some of them even as commensals with living corals. *Tetralia loerentheyi*, at least, may be

suspected of such commensalism, as its living relatives are obligate commensals. The high number of xanthoids is characteristic of any modern coral-associated fauna. The number of dynomenids and dromiids (together 7) may reflect the geological age. The presence of five, perhaps six, porcellanid species (about 10 per cent of the total) and three galatheid species is also peculiar when compared with modern communities. We bring to notice that Dromioidea and Galatheaidea play an important role in Mesozoic and Danian (Early Palaeocene) sponge and coral bearing reef-like communities.

The Priabonian fauna of Facies 4 shares a remarkably low number of species with most other European localities. The exception are the Lutetian and Priabonian faunas of Sicily, described by di Salvo (1933) and Checchia-Rispoli (1905). Of the 17 described species, the following nine are present in the Hungarian fauna: *Palaeomunida defecta*, *Cyamocarcinus angustifrons*, *Gemmellarcarcinus loerentheyi*, *Daira eocaenica* (differing at subspecies level), *Phlyctenodes krenneri*, ?*P. hantkeni*, *Galenopsis similis*, *Lobogalenopsis quadrilobata*, and *Titanocarcinus kochii*.

Species shared with localities in northern Italy (Via, 1969; Busilini *et al.*, 1983) are: *Cyamocarcinus angustifrons*, *Neptocarcinus millenaris* and *Galenopsis similis*, and from Catalonia (Via, 1969) only *Micromaia batalleri*. These may be tabulated as follows:

Table 1.

		N. Italy	Sicily	Spain
	Total no. of spp.	64	17	34
Facies 4	49	3	9 (?8)	1
Facies 5	22	10 (?9)	1	5

Although we have no data concerning the ecological conditions of the Sicilian localities, it seems that these were also reef-like communities, similar to that of Facies 4 of the Szépvölgy Limestone. Apparent endemism of Facies 4 decapods thus most probably reflects the fact that coral-bearing Eocene rocks have seldom been studied for decapods, although, here, Sicily might be an exception. On the other hand this apparent endemism may partly reflect upon the high number of small forms in the Budapest material collected with the aid of magnifying glasses as can be deduced from Table 2.

Table 2. Species according to maximum carapace width or chela length.

	under 10 mm	10-20 mm	over 20 mm
Total in Facies 4	18	16	15
Facies 4 shared with extra-Hungarian localities	-	-	9
Total in Facies 5	-	5	17
Facies 5 shared with extra-Hungarian localities	-	1	12

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