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Systematic Descriptions: Superfamily
Portunoidea

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PART R, REVISED, VOLUME 1, CHAPTER 8T15: SYSTEMATIC DESCRIPTIONS: SUPERFAMILY PORTUNOIDEA

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Classification for this superfamily mainly follows EVANS (2018) with consultation of KARASAWA, SCHWEITZER, and FELDMANN (2008); NG, GUINOT, and DAVIE (2008); SPIRIDONOV, NERETINA, and SCHEPETOV (2014), and DAVIE, GUINOT, and NG (2015).

Superfamily PORTUNOIDEA Rafinesque, 1815

[*nom. transl.* BEURLEN, 1930, p. 354 *ex* Portunidia RAFINESQUE, 1815, p. 97]

Carapace hexagonal, subhexagonal, rectangular, or transversely ovate, generally wider than long but sometimes equant, usually widest at position of last anterolateral spine; front usually with median notch but sometimes entire or with median spine; anterolateral margins almost always spinose, from three to nine spines or lobes; regions poorly to moderately defined, with arcuate epibranchial ridge; lobe on endopod of first maxilliped (so-called portunoid lobe) sometimes present; male sternite 8 indistinctly visible posteriorly, sternal sutures 4/5 through 7/8 usually incomplete, sternite 8 usually visible in ventral view, sometimes with penial groove (Portunidae); telson of male pleon usually reaching posterior end of sternite 4; sutures of male pleomeres, if present, usually immovable; male pleomere 3 almost always with transverse keel; chelipeds usually robust; last pair of pereopods may have ovate dactyls; gonopod 1 usually strongly curved, with inflated, strongly hooked base. [Emended from KARASAWA,

SCHWEITZER, & FELDMANN, 2008, p. 94.]
Upper Cretaceous (Cenomanian)–Holocene.

Family CARCINERETIDAE Beurlen, 1930

[Carcineretidae BEURLEN, 1930, p. 354]

Carapace quadrate, wider than long, flattened longitudinally and transversely; L/W about 90 percent, widest at position of hepatic region, just posterior to post-orbital angle; rostrum straight in dorsal view, strongly downturned in anterior view, downturned portion nearly perpendicular to dorsal carapace; frontal width about half maximum carapace width, outermost edges of front are inner-orbital spines; orbits sinuous, long, with two or three intra-orbital projections and notches; outer-orbital spine triangular, directed forward; fronto-orbital width 90+ percent maximum carapace width; anterolateral and posterolateral margins confluent, lateral margins with blunt protuberances or very short spines; posterolateral reentrants subtle but present; posterior margin rimmed, nearly straight; protogastric regions and hepatic regions with transverse keels or swellings; epibranchial regions arcuate; mesobranchial region and cardiac region with weak transverse ridges; metabranchial region and intestinal region depressed below level of mesobranchial and cardiac regions; sternum ovate, moderately narrow but slightly wider than long; sternites 1 and 2 fused, no evidence of a suture; sternal suture 2/3 complete; sternite 3 with

longitudinal groove extending anteriorly from axis of sternopleonal cavity, sternal suture 3/4 incomplete, well marked; lateral margin of sternite 4 at high angle to axis; sternal sutures 4/5 and 5/6 not parallel, 4/5 at high angle; sternite 8 not visible in ventral view; male pleon with concave margins, reaching to about middle of sternite 4, reaching to about middle of coxae of first pereopods; somites 3–5 appearing to be fused but with clear evidence of sutures; somite 3 very wide, completely filling space between coxae of fifth pereopods; somites 1 and 2 and apparently part of somite 3 not visible in ventral view; somite 3 possibly with transverse keel, other somites appearing to lack transverse keels chelipeds moderately heterochelate; chelae with one or more keels on outer surface; fingers with keels, lacking black tips; propodi of pereopods 2–4 flattened; fourth pereopod with flattened merus and carpus; fifth pereopod with elliptical propodus and dactyl and flattened merus and carpus; propodus not foliaceous, not inserted proximally. [SCHWEITZER, FELDMANN, & KARASAWA, 2007, p. 17; KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 98.] *Upper Cretaceous (Campanian–Maastrichtian)*.

Carcineretes WITHERS, 1922, p. 535 [**C. woolacotti*, p. 535, pl. 16–17; M]. Carapace quadrate, wider than long, flattened longitudinally and transversely; L/W about 90 percent, widest at position of hepatic region, just posterior to postorbital angle; rostrum straight in dorsal view, strongly downturned in anterior view, downturned portion nearly perpendicular to dorsal carapace, dorsal surface of rostrum and surface of downturned portion may be with central tabular regions delineated by grooves; frontal width about 48 percent maximum carapace width, outermost edges of front are inner-orbital spines; orbits sinuous, long, with two or three intra-orbital spines and notches; outer-orbital spine triangular, directed forward; fronto-orbital width 90+ percent maximum carapace width; anterolateral and posterolateral margins confluent, lateral margins with blunt protuberances or very short spines where hepatic region and epibranchial region intersect it; posterolateral reentrants subtle but present; posterior margin rimmed, nearly straight; protogastric regions with transverse keels; hepatic regions with oblique central swelling; epibranchial regions arcuate; urogastric region narrower than mesogastric and cardiac, defined laterally by deep branchiocardiac grooves; mesobranchial region and cardiac region inflated into almost ridge-like

structure continuous across carapace; metabranchial region and intestinal region depressed below level of mesobranchial and cardiac regions; sternum ovate, slightly wider than long; sternites 1 and 2 fused, no evidence of a suture; sternal suture 2/3 complete; sternite 3 with longitudinal groove extending anteriorly from axis of sternopleonal cavity, sternal suture 3/4 incomplete, notch in margin; lateral margin of sternite 4 at high angle to axis; sternal suture 4/5 and 5/6 not parallel, 4/5 at high angle; sternite 8 not visible in ventral view; male pleon with concave margins, reaching to about middle of sternite 4, reaching to about middle of coxae of first pereopods; somites 3–5 fused, may be slight evidence of sutures; somite 3 very wide, completely filling space between coxae of fifth pereopods; somites 1 and 2 and apparently part of somite 3 not visible in ventral view; somites appearing to lack transverse keels; chelipeds weakly heterochelate; chelae with keel or keels on outer surface; fingers with keels, lacking black tips; fourth pereopod with flattened carpus and merus; fifth pereopod with elliptical dactyl and propodus and flattened carpus and merus. [Emended from SCHWEITZER, FELDMANN, & KARASAWA, 2007, p. 19.] *Upper Cretaceous (Maastrichtian)*: Belize, Jamaica, Mexico (Chiapas).—FIG. 1,1. **C. woolacotti*, holotype NHMUK In.20780, Maastrichtian, Jamaica, scale bar, 1 cm (new).

Cancrinxantho VAN STRAELEN, 1934, p. 3 [**C. pyrenaicus*, p. 3, fig. 2; M]. Orbits wide, rostrum extremely narrow, eyestalks long, well calcified; hepatic and branchial regions with transverse ridges; posterolateral margins with long spines. [SCHWEITZER, FELDMANN, & KARASAWA, 2007, p. 20.] *Upper Cretaceous (Campanian)*: Spain.—FIG.1,2. **C. pyrenaicus*, cast of a plaster cast of holotype, now in MGSB, but numbered KSU D 204, scale bar, 1 cm (new).

Mascaranada VEGA & FELDMANN, 1991, p. 172 [**M. difuntaensis*, p. 173, fig. 7; OD]. Carapace subhexagonal to ovate, wider than long, widest near midlength; regions well defined by deep grooves; rostrum and orbits narrow, orbit with small outer-orbital spine; anterolateral margin entire, convex; posterolateral margins nearly straight, converging posteriorly; protogastric, hepatic, epibranchial, mesobranchial, and cardiac regions with transverse ridges; fifth pereopods with elliptical propodi and dactyli. [Emended from VEGA & FELDMANN, 1991, p. 172.] *Upper Cretaceous (Maastrichtian)*: Mexico (Nuevo León).—FIG.1,3. **M. difuntaensis*, holotype IGM-5204, scale bar, 1 cm (Vega & Feldmann, 1991, fig. 7.1).

Family CARCINIDAE MacLeay, 1838

[Carcinidae MACLEAY, 1838, p. 59] [=Megalopidae HAWORTH, 1825, p. 184; =Platyonichidae DANA, 1851, p. 130; =Portumninae ORTMANN, 1899, p. 1170; =Xaividae BERG, 1900, p. 224]

Carapace hexagonal to subcircular, usually wider than long; frontal margin with two

to four spines or entire, shorter than posterior margin; orbits with one or two fissures which may be reduced or absent; anterolateral margin with four or five spines or lobes excluding outer-orbital spine; posterolateral reentrant well or poorly developed, sometimes absent; basal antennal article fixed; chelipeds usually heterochelous, sometimes isochelous; manus sometimes with proximal spine; proximal inner surface of fixed finger concave; carpus usually with outer spine; merus usually without spines; meri of pereopods 2–5 usually without distal spines; dactyl of pereopod 5 variable, may be ovate, styliform, ensiform, or lanceolate; sternal sutures usually at least partially incomplete, sometimes all complete (Pirimelinae); male pleonal somites 3–5 usually fused but sometimes with visible sutures, rarely all free (Thiinae); male gonopod one straight or curved, sometimes with spines or setae; male gonopod 2 longer than 1. [Emended from EVANS, 2018, p. 40.] *Lower Cretaceous (Albian)–Holocene.*

Subfamily CARCININAE MacLeay, 1838

[*nom. transl.* ALCOCK, 1899, p. 7 *ex* Carcinidae MACLEAY, 1838, p. 59]

Carapace subhexagonal, somewhat wider than long or about as wide as long, length ranging from 80 to 100 percent maximum width; front with five lobes including inner orbital lobe, or nearly straight; front about one-quarter to one-third maximum carapace width; orbits small, orbital fissures reduced, fronto-orbital width about half maximum carapace width; anterolateral margin with five or fewer spines including outer-orbital spine; axial regions generally well developed; carapace with arcuate epigastric ridge; posterolateral reentrant reduced or absent; posterior margin convex, not distinctly differentiated from posterolateral margin; basal antennal article narrow, fixed, longer than wide; portunid lobe not well developed; chelipeds shorter than at least one other pereopod, generally smooth except for a spine on carpus; propodi of pereopod 4 may be ovate; dactyli of pereopod 5 styliform, ensiform, or lanceolate; male gonopod 1

without subterminal spines; sternite 8 not visible in ventral view; sternal sutures 4/5, 5/6, and 6/7 interrupted, sternal suture 7/8 continuous; male pleon ranging from broadly triangular to narrow and nearly uniform in width; male pleonal somites 3–5 fused; male pleonal somite 3 widened laterally, with keel; anterior margin of somite 6 concave forward; posterior margin of telson convex posteriorly to fit into somite 6. [Compiled from STEPHENSON & CAMPBELL, 1960, p. 76; APEL & SPIRIDONOV, 1998, p. 181; DAVIE, 2002, p. 450; POORE, 2004, p. 409; KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 99.] *Eocene (Ypresian)–Holocene.*

Carcinus LEACH, 1814, p. 390, *non Carcinus* LATREILLE, 1796, p. 197, suppressed by ICZN Opinion 330, 1955, p. 323 [**Cancer maenas* LINNAEUS, 1758, p. 627, M; validated by ICZN Opinion 330, 1955, p. 323] [= *Ligia* WEBER, 1795, p. 92 (type, *Cancer granarius* HERBST, 1783 in 1782–1804, p. 107, pl. 2, 28, M); = *Megalopa* LEACH, 1814, p. 431 (type, *Cancer maenas*, SD MANNING & HOLTHUIS, 1981, p. 75); = *Macropa* LATREILLE, 1822, p. 9 (type, *Megalopa montagui* LEACH, 1817 in 1815–1875, text to pl. 16, 14, M; = *Sympractor* GISTEL, 1848, p. ix (type, *Cancer maenas* [LINNAEUS] M); = *Carcinides* RATHBUN, 1897, p. 164 (type, *C. maenas* [LINNAEUS], M)]. [See MANNING & HOLTHUIS, 1981, for full species synonymy.] Carapace hexagonal, not much wider than long; front with five spines including inner orbital spines; orbits with one fissure; anterolateral margins with five spines including outer-orbital spine, last spine smallest, first four broad, triangular; posterolateral margin concave, posterolateral reentrants present; posterior margin straight; regions poorly defined; dactyl of fifth pereopod lanceolate. *Oligocene–Holocene.* *Oligocene:* USA (California). *Pliocene:* UK (England, Ireland, Scotland). *Holocene:* Cosmopolitan.—FIG. 1, 4a–b. **C. maenus* (LINNAEUS), USNM 258383, Holocene, Portugal, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Cicarnus KARASAWA & FUDOUJI, 2000, p. 244 [**C. fumiae*; OD]. Carapace hexagonal, slightly wider than long, weakly vaulted transversely and longitudinally; fronto-orbital margin about 60 percent, maximum carapace width; orbits with one fissure and broad, triangular outer-orbital spine; anterolateral margins with five spines including outer-orbital spine, fourth spine appears to be very small, second and third broadly triangular; protogastric regions with transverse ridges; epibranchial region moderately inflated. *Eocene (Bartonian):* Japan.—FIG. 1, 5. **C. fumiae*, holotype MFM 218512, scale bar, 1 cm (new).

Miopipus MÜLLER, 1984, p. 84 [**Portunus pygmeus* BROCCHI, 1883, p. 1, pl. 5, 4; OD]. Carapace

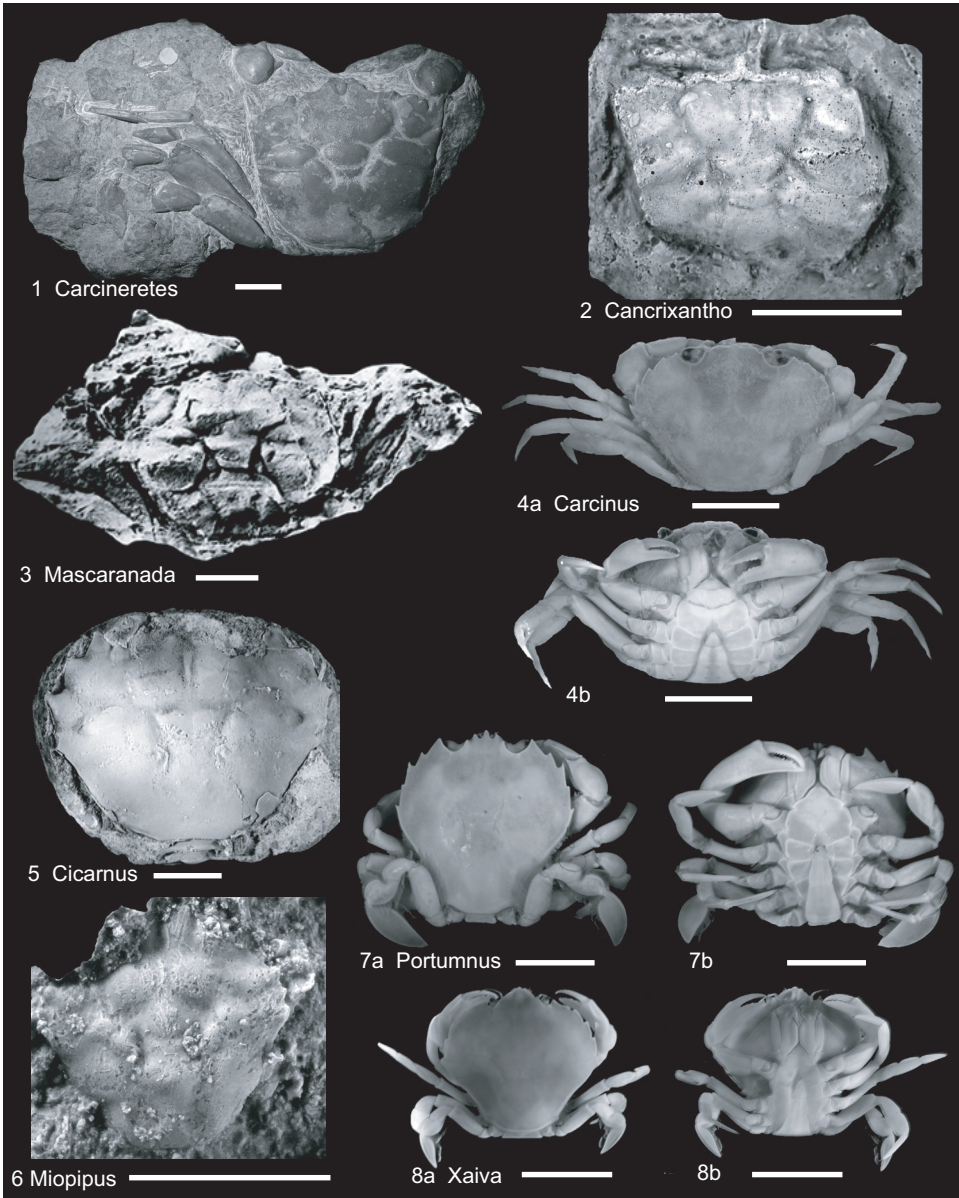


FIG 1. Carcineretidae, Carcinidae (p. 2–5).

about as wide as long, ovate; front with three lobes; orbits deep, forward directed; anterolateral margin subparallel, with five spines including outer-orbital spine, spine small, all about same size; posterolateral margins converging posteriorly, posterior reentrant present, posterior margin narrow; regions moderately defined. *Eocene–Miocene. Eocene (Ypresian)*: Italy. *Miocene (Langhian)*: Hungary.—FIG.1,6. **M. pygmeus* (BROCCHI), KSU D 104,

cast of M86.27, Langhian, Hungary, scale bar, 1 cm (new).

Portumnus LEACH, 1814, p. 429 [*Cancer latipes* PENNANT, 1777, p. 3; M; =*Cancer variegatus* LEACH, 1814, p. 391] [=*Platyonichus* LATREILLE, 1818, p. 4 (type, *C. latipes* [PENNANT]; OD)]. Carapace about as wide as long, ovate, regions poorly or not defined; front with five lobes including small inner-orbital lobes; orbits wide, circular, forward

directed; anterolateral margin with five short, forward-directed spines including outer-orbital spine; posterolateral margin concave, rimmed, posterior margin convex, rimmed; dactyls of fifth pereiopod lanceolate. *Miocene–Holocene. Miocene (Langhian)*: Hungary. *Holocene*: North Atlantic, Mediterranean Sea.—FIG. 1,7*a–b*. **P. latipes* (PENNANT), USNM 20296, Holocene, English Channel, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (new).

Xaiva MACLEAY, 1838, p. 62 [**X. pulchella*; M (ICZN Opinion 712, 1964); =*Portunus biguttatus* RISSO, 1816, p. 31] [=Portunoides BOHN, 1902, p. 448 (type, *P. garstangi*, M, =*Portunus biguttatus* RISSO)]. Carapace slightly wider than long, ovate, regions weakly defined; front projected beyond orbits, with three stronger central projections and two weak projections forming inner-orbital spines for a total of five; orbits narrow, with two fissures; anterolateral margins with six spines including small outer-orbital spine; last spine with short ridge extending onto carapace; posterolateral margin weakly concave, rimmed; posterior margin convex, rimmed; dactyls of fifth pereiopod ensiform. *Miocene–Holocene. Miocene (Langhian)*: Hungary, Malta. *Holocene*: North Atlantic Ocean, coastal Africa, Mediterranean Sea.—FIG. 1,8*a–b*. **X. biguttata* (RISSO), USNM 14499, Holocene, Italy, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (new).

Subfamily COELOCARCININAE

Števíč, 2005

[*nom. transl.* EVANS, 2018 ex Coelocarcinini ŠTEVÍČ, 2005, p. 85]

Carapace rounded, about as wide as long; front produced beyond orbits, blunt; orbits very small; anterolateral margins crispate, with four or five weak lobes separated by fissures; posterolateral margin strongly concave; chelipeds short; propodus and dactylus of pereiopod 5 ovate; sternal sutures 4/5 and 5/6 discontinuous; suture 6/7 continuous; male pleonal somites 3–5 fused, no sutures visible. [Emended from NG, 2002.] *Holocene*.

Coelocarcinus EDMONDSON, 1930, p. 13 [**C. foliatus*; M]. As for subfamily. *Holocene*: West-Central Pacific Ocean, Indian Ocean, Madagascar.—FIG. 2,1*a–b*. **C. foliatus*, USNM 143987, Holocene, Madagascar, dorsal (*a*) and ventral (*b*) views, scale bars, 1 cm (new).

Subfamily PRIMELINAE Alcock, 1899

[Primelinæ ALCOCK, 1899, p. 95]

Carapace hexagonal, about as long as wide, regions well defined; front with five spines

including inner-orbital spine, three middle spines produced forward beyond orbits; orbits oblique, directed anterolaterally or directed forward; anterolateral margins with five spines including outer-orbital spine; posterolateral margin generally concave, somewhat shorter than anterolateral margin; pereiopod 5 with styliform dactylus; sternal sutures 4/5 through 7/8 complete; male pleonal somites 3–5 fused, no sutures visible, telson long, sharp. [Emended from DAVIE, GUINOT, & NG, 2015, p. 1102]. *Miocene–Holocene*.

Pirimela LEACH, 1816 in 1815–1875, text to pl. 3 [**Cancer denticulatus* MONTAGU, 1808, p. 87; M (ICZN Opinion 73, 1922, p. 28); =*Pirimela princeps* HOPE, 1851, p. 4] [=*Perimela* AGASSIZ, 1846, unnecessary emendation]. Carapace slightly wider than long, orbits directed forward, with intra-orbital spine bounded by fissures; anterolateral spines large, triangular; carapace regions ornamented with short, scabrous ridges posteriorly; chelipeds short, small, isochelous. *Miocene–Holocene. Miocene (Langhian)*: Hungary. *Holocene*: Mediterranean Sea, northeastern Atlantic Ocean.—FIG. 2,2. **P. denticulata*, Holocene, southern North Sea, drawing of photo by Hans Hillewort, CC BY-SA 4.0, no scale available (new; C. E. Schweitzer).

Parapirimela VAN STRAELEN, 1937, p. 1 [**P. angolensis*; M]. Based on an incomplete specimen; whereabouts of type unknown. Front apparently sulcate; orbits forward directed, possibly with intra-orbital spines; carapace regions well defined. *Miocene*: Angola.—FIG. 2,3. **P. angolensis*, scale bar, 1 cm (Van Straelen, 1937, fig. 1).

Pliopirimela VAN BAKEL, JAGT, FRAAIJE, & WILLE, 2003, p. 104 [**P. deconincki*, p. 104, pl. 6,1–3; OD]. Carapace hexagonal; front with central spine well produced beyond other spines; orbits forward directed, with one fissure; anterolateral margins shorter than posterolateral margins with five triangular spines of equal size including outer-orbital spine; posterolateral margins long, straight; posterior margin straight, rimmed; axial regions with three tubercles, branchial regions with row of tubercles subparallel to axis. *Pliocene (Piacenzian)*: Belgium.—FIG. 2,4. **P. deconincki*, holotype, MAB k.2387, scale bar, 1 cm (Van Bakel & others, 2003, pl. 6,3).

Trachypirimela MÜLLER, 1974a, p. 278 [**T. radula*, p. 278, pl. 2,5–6; OD; =*Micromithrax grippi* MÜLLER, 1974a, p. 279, pl. 2,1–2]. Carapace longer than wide, front with five spines; anterolateral margin with five spines, 1/2 and 4/5 closely spaced; posterolateral margins weakly concave; regions well defined. *Miocene (Langhian)*: Hungary.—FIG. 2,5. **T. grippi* (MÜLLER), KSU D 1512, scale bar, 5 mm (new).

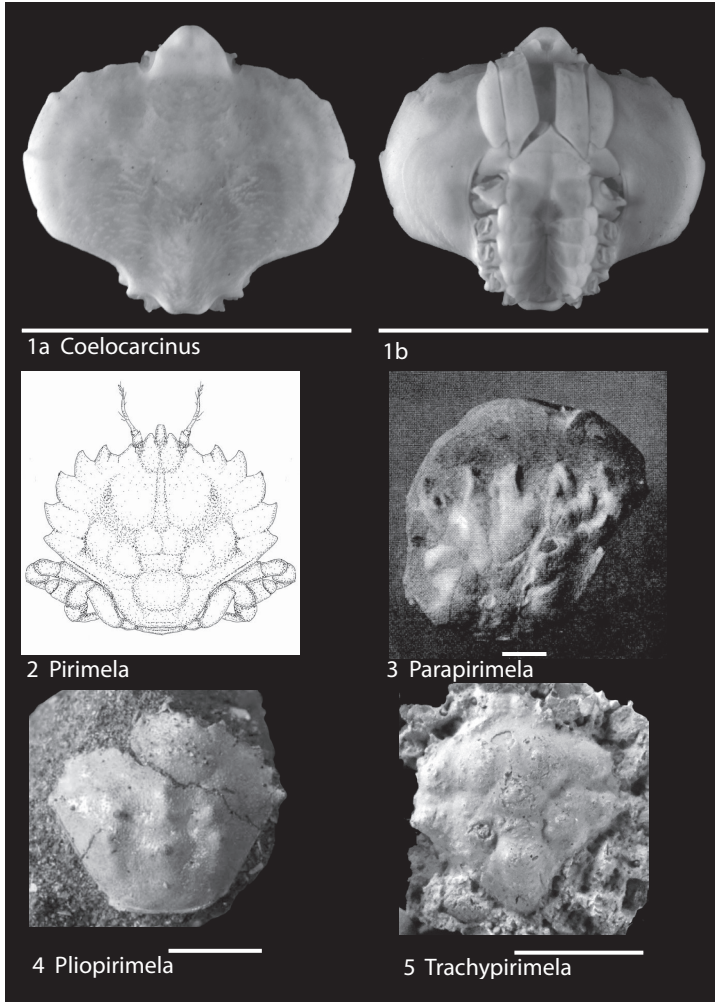


FIG 2. Carcinidae (p. 5).

Subfamily POLYBIINAE Paul'son, 1875

[*nom. correct.* ORTMANN, 1893, p. 66 *pro* Polybiinae PAUL'SON, 1875, p. 69] [=Coenophthalmoida ALCOCK, 1899, p. 8; =Lio-carcininae RATHBUN, 1930, p. 18; =Macropipinae STEPHENSON & CAMPBELL, 1960, p. 88]

Carapace moderately broad, length about 65–80 percent maximum carapace width, widest between 50–60 percent the distance posteriorly, sometimes with longitudinal branchial ridges parallel to axis, often with large granules or tubercles ornamenting carapace; orbits usually moderate sized, with two fissures, fronto-orbital width usually 50–60 percent maximum carapace

width, rarely approaching 90 percent (some *Archaeogeryon*); front spined, number and size of spines variable, usually with axial notch but sometimes with axial spine (*Macropipus*), front ranging from 20–40 percent maximum carapace width; anterolateral margins with three to five spines including outer-orbital spine, last anterolateral spine often long and directed laterally; epibranchial ridge arcuate, extending from last anterolateral spine to axial regions; large posterolateral reentrant for insertion of last pereopods; male pleonal somites 3–5 fused and usually with clear evidence of sutures or indentations

in the margins marking the position of somites or all male somites free, somite 3 and sometimes others with transverse keels, somite 3 generally markedly wider than other somites, telson extending to middle or anterior of sternite 4; median groove present on male sternite 3; portion of male sternite 8 usually visible in ventral view but sometimes completely obscured by pleon; sternal sutures appearing to be incomplete; portunid lobe usually present; basal antennal article fixed or free, usually lacking laterodistal spines; chelae usually keeled; some pereopods as long as cheli-peds; dactylus of fifth pereopod oblancoolate or obovate, very rarely ovate and paddle-like in traditional sense (*Parathranites*). [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 101.] *Lower Cretaceous (Albian)—Holocene.*

Archaeogeryon COLOSI, 1924, p. 250 [**A. fuegianus*, p. 251, fig. 1–5; M] [= *Proterocarcinus* FELDMANN, CASADÍO, CHIRINO-GÁLVEZ, & AGUIRRE-URRETA, 1995, p. 9 (type, *P. lophos*, OD)]. Carapace transversely ovoid to hexagonal, wider than long, 0.60–0.76 times as long as wide; front narrow, down turned, bearing four spines including outer-orbital spines; orbits extremely wide, rimmed, bearing two orbital fissures, one at about midlength and the other near the outer orbital corner; fronto-orbital width to width ratio 0.68–0.95; anterolateral margin short, with two to five spines including outer-orbital spines; epibranchial ridge elevated, granular, terminating at anterolateral corner; branchial region swollen, with longitudinal ridge parallel to long axis of cardiac region; first pereopods isochelous; propodus and dactylus of fifth pereopod paddle-like. [FELDMANN & others, 2011, p. 102.] *Paleocene–Miocene. Paleocene (Danian):* Argentina. *Oligocene:* Argentina. *Miocene:* Argentina, Chile.—FIG. 3, 1*a–b*. *Archaeogeryon lophos*, holotype MLP 8769, Danian, Argentina, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (Feldmann & others, 1995, fig. 5).

Bathynectes STIMPSON, 1871, p. 145 [**B. longispina*; p. 146; SD RATHBUN, 1930, p. 27; = *Geryon incertus* MIERS, 1886, p. 224] [= *Thranites* BOVALLIUS, 1876, p. 61–63, pl. 14–15 (type, *T. velox*, M)]. Carapace hexagonal, regions moderately defined, with a ridge across midlength of carapace extending from last anterolateral spine across mesogastric region and through arcuate branchial region; anterolateral margin with three spines including outer-orbital spine, last spine long; front with five spines including inner orbital spines, fronto-orbital width about 60 percent maximum carapace width, orbits with two closed fissures; cardiac region wide; merus of chelipeds with long anteriorly directed spine.

Miocene–Holocene. Miocene (Langhian–Serravalian): Ukraine. *Pleistocene:* Italy. *Holocene:* Atlantic, Mediterranean.—FIG. 3, 2*a–b*. **B. longispina*, USNM 168042, Holocene, Florida, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (new).

Bericocarcinus DE ANGELI, 2018, p. 34 [**B. alontensis*, p. 34, fig. 2; OD]. Carapace about as wide as long; front wide; orbits wide and widely spaced, with two open fissures, fronto-orbital width about 75 percent maximum carapace width; anterolateral margins with 4 wide spines including outer-orbital spine; carapace regions weakly developed, hepatic and epibranchial regions most defined; posterolateral margins straight and parallel to one another; posterior margin wide. *Eocene (Priabonian):* Italy.—FIG. 3, 3. **B. alontensis*, holotype MCZ 5746, scale bar, 5 mm (new, photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).

Boschetti BUSULINI, TESSIER, BESCHIN, & DE ANGELI, 2003, p. 14 [**B. giampietroi*, p. 15, fig. 2–4; OD]. Carapace hexagonal, regions moderately well marked, densely ornamented with tubercles of varying sizes; front quadrilobed; orbits broad, upper orbital margin with three small intra-orbital spines, outer-orbital spine long, directed forward, fronto-orbital width about 85 percent maximum carapace width; anterolateral margins short, with five spines including outer-orbital spine, first three about equal in size, fourth long, directed laterally, fifth small, directed laterally; posterolateral margins sinuous; posterior margin wide, straight; protogastric, mesogastric, cardiac, and epibranchial regions with large spherical swellings centrally. *Eocene (Ypresian–Lutetian):* Italy.—FIG. 3, 4. **B. giampietroi*, holotype MCZ 2401, scale bar, 1 cm (new; photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).

Coeloma A. MILNE-EDWARDS, 1865, p. 324 [**C. vigil*, p. 324, pl. 12; M] [= *Litoricola* WOODWARD, 1873, p. 28–30, pl. 2, 2–5 (type, *L. dentata*, SD GLAESSNER, 1929, p. 237); = *Coeloma (Paracoeloma)* LÖRENTHEY & BEURLIN, 1929, p. 244 (type, *Coeloma rupeliense* STAINIER, 1887, p. 86, pl. 5, OD); = *Coeloma (Interocoeloma)* POLKOWSKY, 2005, p. 48 (type, *Coeloma tauricum* VON MEYER, 1862, p. 174, pl. 19, 10, M)]. Carapace hexagonal, wider than long, length about three-quarters carapace width, flattened transversely and vaulted longitudinally; front narrow, with four blunt spines including inner orbital spines which are directed anterolaterally, about 20 percent maximum carapace width; orbits very wide, with beaded rim, upper-orbital margin biconcave, with two fissures; fronto-orbital width about 80 percent maximum carapace width; outer-orbital spine directed forward; anterolateral margins with three spines excluding outer-orbital spine; posterolateral margins nearly straight, about twice as long as anterolateral margins; posterior margin straight, rimmed; posterolateral reentrants shallow; epigastric regions longitudinally ovoid; branchiocardiac groove deep, defining margins of metagastric and urogastric regions; regions

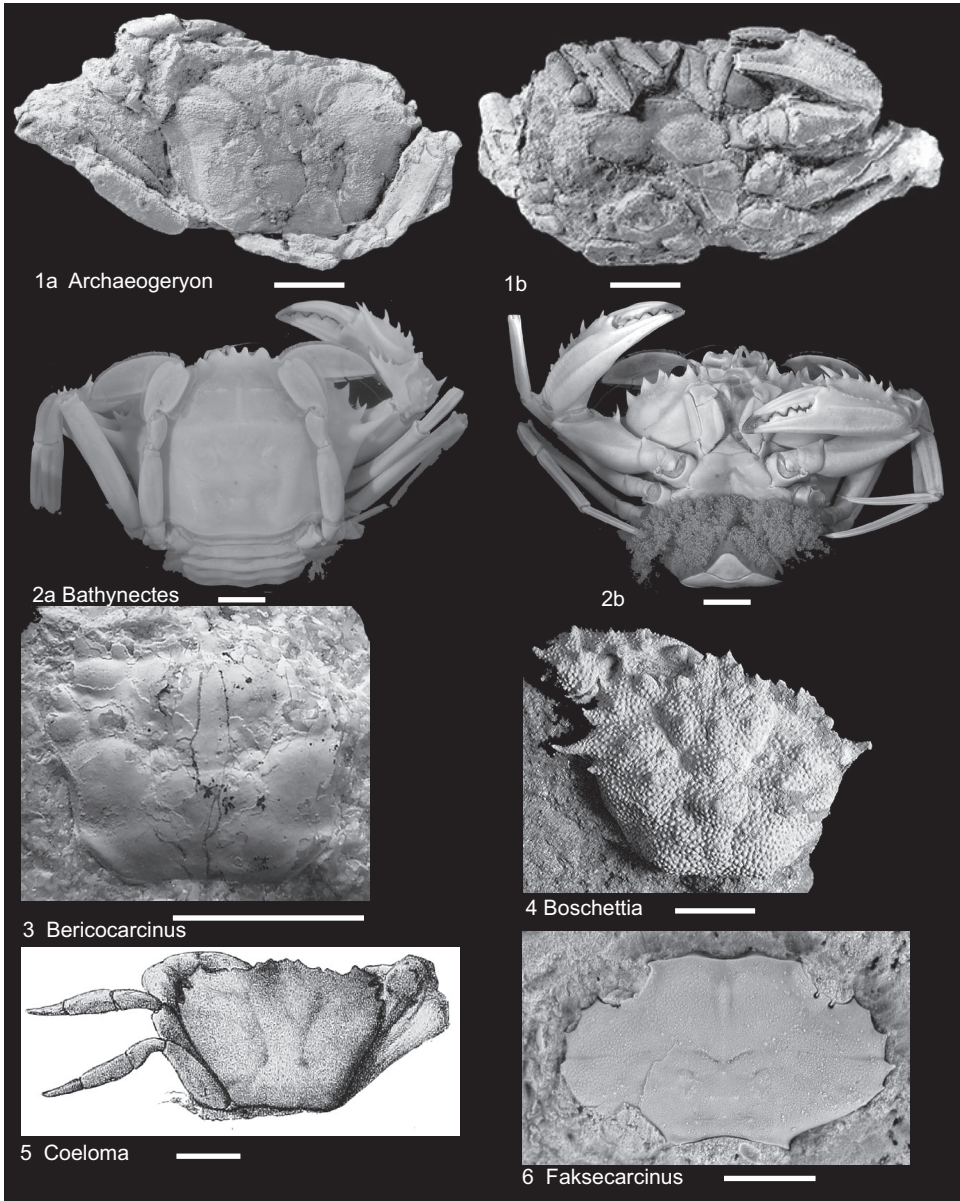


FIG 3. Carcinidae (p. 7–9).

uniformly granular; sternum broad, ovate; sternites 1 and 2 fused, sternal sutures 2/3 entire, remainder interrupted except 7/8 and possibly 6/7. [Diagnosis based on type species; genus may be polyphyletic as currently construed.] Ranges for *Coeloma sensu stricto*: *Eocene–Miocene*. *Eocene*: Italy. *Oligocene (Rupelian)*: Belgium, France, Germany, Italy, The Netherlands. *Oligocene*: Italy, Slovakia. *Miocene*

(*Burdigalian*): Hungary. Ranges for *Coeloma sensu lato* (including *Litoricola*): *Paleocene–Pliocene*. *Paleocene (Selandian)*: France. *Paleocene*: USA (California). *Eocene (Ypresian)*: Greenland, UK (England). *Lutetian*: Germany. *Oligocene (Rupelian)*: Belgium, Germany. *Oligocene (Chattian)*: Germany, Hungary. *Paleogene*: Russia. *Miocene*: Denmark. *Pliocene*: Italy.—FIG. 3,5. *C. dentata*

- (WOODWARD), Eocene, UK (England), scale bar, 1 cm (Woodward, 1873, pl. 2,3).
- Faksecarcinus** SCHWEITZER, FELDMANN, FRANȚESCU, & KLOMPMAKER, 2012, p. 151 [*Xanthosia gracilis* JAKOBSEN & COLLINS, 1997, p. 95, pl. 2,1–2; OD]. Carapace ovate, wider than long, length about 60 percent maximum width, widest about two-thirds the distance posteriorly on carapace at position of last anterolateral spine; front broadly bilobed, front wide, about 40 maximum carapace width; orbits deep laterally, directed obliquely anterolaterally, with two open fissures, fronto-orbital width 70 percent maximum carapace width; anterolateral margins with four spines including outer-orbital spine, spines increasing in size posteriorly, last spine long, attenuated; carapace regions developed as weak, broadly inflated areas; muscle scars prominent on metagastric, mesogastric, and branchial regions. [SCHWEITZER & others, 2012, p. 151.] *Lower Cretaceous–Paleocene. Lower Cretaceous (Albian)*: Spain. *Paleocene (Danian)*: Denmark.—FIG. 3,6. *F. koskobilensis* (KLOMPMAKER & others, 2011), MAB k2563A, Albian, Spain, scale bar, 1 cm (new; photo by A. A. Klompmaker, University of Alabama, Tuscaloosa, Alabama, USA).
- Falsiportunites** COLLINS & JAKOBSEN, 2003, p. 72 [*F. longispinosus*, p. 72, pl. 4,1–6; OD]. Carapace hexagonal; front with four small, blunt projections, otherwise straight; orbits wide, with two short fissures, fronto-orbital width about two-thirds maximum carapace width; anterolateral margins with five spines including outer-orbital spines, last spine extremely long and attenuated, directed slightly upward and extending into epibranchial ridge on dorsal carapace; posterolateral margins straight, posterolateral reentrant large, posterior margin straight; carapace regions well defined; branchial regions with two large spherical swellings axially; pleonal somites 3–5 with transverse ridges, male pleonal somites 3–5 free or with very clear sutures; small portion of sternite 8 visible in ventral view. *Eocene (Ypresian–Lutetian)*: Denmark.—FIG. 4,1a–b. **F. longispinosus*, cast of holotype MGUH 26787, a, dorsal carapace and appendages; b, ventral surface; scale bars, 1 cm (new; photo by S. Jakobsen, Geomuseum Fakse, Denmark).
- Liocarcinus** STIMPSON, 1871, p. 146 [*Portunus bolsatus* FABRICIUS, 1798, p. 366; OD]. Carapace not much wider than long; front with three or five spines including inner-orbital spines; orbits forward directed, with two fissures; anterolateral margins with five spines including outer-orbital spine; regions moderately well marked, may be ornamented with transverse ridges or scabrous granules; posterolateral reentrant present, large; dactyls of fifth pereiopod ovate. *Eocene–Holocene. Eocene (Lutetian)*: Italy. *Oligocene (Rupelian)*: France. *Oligocene*: Romania. *Miocene (Tortonian)*: Austria, Hungary. *Miocene (Langhian)*: Hungary, Poland. *Miocene*: Austria. *Pliocene (Zanclan)*: Italy. *Pliocene Piacenzian*: Belgium. *Pliocene*: UK (England). *Pleistocene*: UK (England). *Cenozoic*: Azerbaijan.
- Holocene*: West Pacific Ocean, North Atlantic Ocean, Mediterranean Sea, African coast.—FIG. 4,2a–b. **L. bolsatus*, USNM 106462, Holocene, North Atlantic Ocean, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).
- Lovaroides** BESCHIN, DE ANGELI, CHECCHI, & ZARANTONELLO, 2016, p. 64 [**L. elegans*, p. 64, pl. 12,1–3; OD]. Carapace about as wide as long; front sinuous, with four blunt lobes including inner-orbital angle; orbits shallow; anterolateral margins with two long lobes and two small blunt spines; epibranchial region developed as transverse, low ridge; cardiac region wide, transversely inflated. *Eocene (Lutetian)*: Italy.—FIG. 4,3. **L. elegans*, holotype MCZ 3949, scale bar, 1 cm (new; photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).
- Macropipus** PRESTANDREA, 1833, p. 5 [*Portunus macropipus*, p. 4; M (ICZN Opinion 394, 1956, p. 317); =*Portunus tuberculatus* ROUX, 1830 in 1828–1830, pl. 32,1–5] [=*Elliptodactylus* DOBLEIN, 1904, p. 93–94, pl. 30,1–3, pl. 32,7 (type, *E. rugosus*, M)]. Carapace not much wider than long; front with five spines including inner orbital spines, projecting beyond orbits; anterolateral margin with five spines including outer orbital spine; posterolateral margin concave; posterolateral corner with small blunt protuberance; posterior margin convex; carapace ornamented with transverse, setose ridges; first pereiopods isochelous. ?*Eocene–Holocene. ?Eocene*: Italy. *Miocene (Langhian–Serravallian)*: Switzerland. *Pleistocene*: Italy. *Holocene*: Eastern Atlantic Ocean, Mediterranean Sea.—FIG. 4,4a–b. *Macropipus australis* GUINOT, 1961, paratype MNHN IU 2014 22933, Holocene, South Atlantic, dorsal (a) and ventral (b) views, scale bars, 1 cm (© MNHN, Project Reolnat, N. Mollaret).
- Maeandricampus** SCHWEITZER & FELDMANN, 2002, p. 955 [*Portunites triangulum* RATHBUN, 1926, p. 68, pl. 17,3–6; OD]. Carapace wider than long, length about 65 percent maximum carapace width, carapace widest at position of last anterolateral spine; front with six spines including inner-orbital spines; orbits with two fissures; anterolateral margins with five spines including outer-orbital spine, last spine longest, projected laterally, extending onto dorsal carapace as arcuate epibranchial ridge; posterolateral margin weakly convex, posterolateral reentrant moderately large; region moderately defined, third and fourth anterolateral spine extending onto hepatic region as short ridges; branchial regions with two or three large tubercles axially; cardiac region with two tubercles; branchial regions with longitudinal ridge; paddle-like dactyl of fifth pereiopod. *Eocene (Bartonian)*: New Zealand. *Oligocene*: Mexico (Baja California Sur). *Oligocene–Miocene*: USA (Washington).—FIG. 4,5. *M. starri* FELDMANN, SCHWEITZER, & GOEDERT, 2018, paratype UWBM 100632, Miocene, Washington, USA, scale bar, 1 cm (new).
- Megokkos** SCHWEITZER & FELDMANN, 2000, p. 640 [*Portunites alaskensis* RATHBUN, 1926, p. 72, pl.

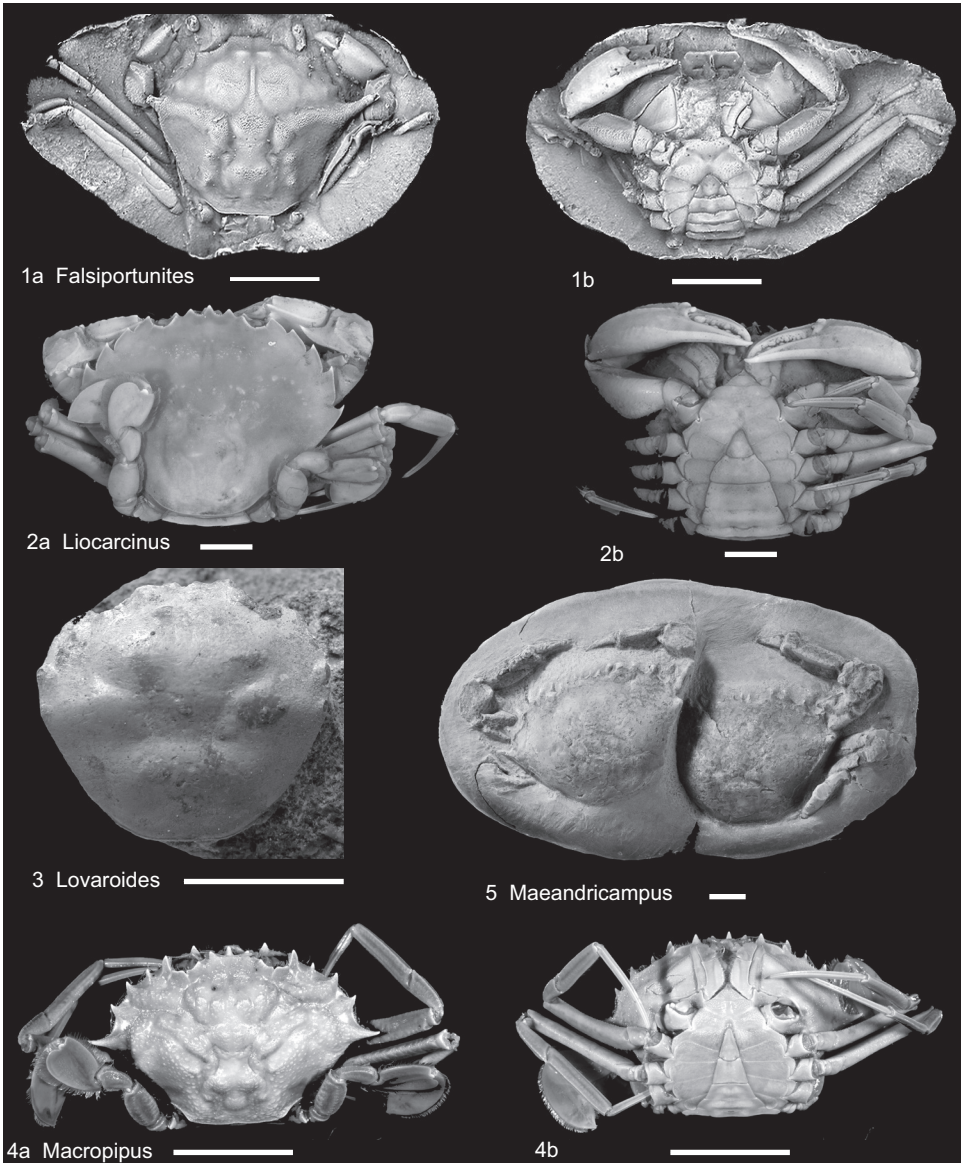


FIG 4. Carcinidae (p. 9).

18,3–4, pl. 22,3; OD]. Carapace wider than long, hexagonal, length about 65 percent maximum width; regions moderately defined by shallow grooves; front broad, nearly straight, with central, triangular, blunt protuberance or four blunt protuberances; orbits very wide; fronto-orbital width two-thirds to three-quarters maximum carapace width but may reach 90 percent maximum carapace width; orbits very wide, deep, sometimes with small intra-orbital spine and notch, two orbital fissures or notches (one of which is notch adjacent to intra-

orbital spine if present); anterolateral margin short, with three or four spines excluding outer-orbital spine, last spine usually longest; protogastric and hepatic regions with transverse ridges; epibranchial region arcuate; branchial regions weakly inflated; posterolateral reentrant large, well developed; chelipeds heterochelous, stout; fingers with large, blunt denticles on occlusal surface; dactyl of fifth pereiopod paddle-like. *Eocene–Oligocene*. *Eocene* (*Priabonian*): Japan, USA (Washington). *Eocene*: Argentina. *Oligocene*: Canada (British Columbia),

- USA (Alaska, Oregon, Washington).—FIG. 5, 1a–b. *Megokkos macrospinus* SCHWEITZER, FELDMANN, TUCKER, & BERGLUND, 2000, Eocene, Washington, USA, *a*, USNM 50786, dorsal carapace; *b*, USNM 507810, ventral surface, scale bars, 1 cm (Schweitzer & Feldmann, 2000, fig. 2 and 1, respectively).
- Minohellenus** KARASAWA, 1990, p. 21 [**Charybdis* (*Minohellenus*) *quinquedentata*, p. 21, pl. 6, 7–8; OD] [= *Itoigawaiia* KARASAWA, SAKUMOTO, & TAKAYASU, 1992, p. 455 (type, *Portunites minoensis* KARASAWA, 1990, p. 14, pl. 2, 1, 3–5; OD); = *Imaizumila* KARASAWA, 1993, p. 52 (type, *I. sexdentata*, p. 52, pl. 11, 1–3, OD)]. Carapace hexagonal, widest at position of last anterolateral spine; carapace regions poorly defined; frontal margin with six triangular spines including inner orbital spines; orbits circular, directed forward, with two orbital fissures; anterolateral spines long, triangular, sharp, last spine typically longest; protogastric region weakly inflated, hepatic region flattened; chelae heterochelate, smooth or with granular keels on outer surface. *Eocene–Miocene*. *Eocene*: Chile, USA (California). *Oligocene* (*Rupelian–Chattian*): Japan. *Oligocene*: Chile. *Miocene*: Chile, Japan.—FIG. 5, 2a–b. **M. quinquedentatus*, KMNH IvP 300,020, Oligocene, Japan, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (new).
- Necora** HOLTHUIS, 1987, p. 3 [**Cancer puber* LINNAEUS, 1767, p. 1046; OD; = *Cancer velutinus* PENNANT, 1777, p. 4]. Carapace slightly wider than long; frontal margin with four spines not including orbital spines; upper orbital margin with two open fissures; anterolateral margin with five spines including outer-orbital spine, generally of about equal size, last anterolateral spine extending onto dorsal carapace as epibranchial ridge; posterolateral margins long, straight, posterolateral reentrants large; posterior margin straight; carapace regions poorly defined; manus and dactyl of fifth pereiopod paddle-like. *Pliocene–Holocene*. *Pliocene–Pleistocene*: UK (England). *Holocene*: Northeastern Atlantic Ocean, Mediterranean Sea.—FIG. 5, 3a–b. **N. puber* (LINNAEUS), USNM 57423, Holocene, Gibraltar, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (new).
- Ophthalmoplax** RATHBUN, 1935, p. 52 [**O. stephensoni*; p. 52, pl. 13, 13–18, pl. 26, 10; OD]. Carapace nearly square, slightly wider than long, widest at position of last anterolateral spine, about 40 percent the distance posteriorly; front with two axial spines set well below level of outer two blunt spines which are inner-orbital spines, front about 20 percent maximum carapace width; orbits very broad, upper-orbital margin sinuous, with two intra-orbital spines, outer-orbital spine directed forward, fronto-orbital width about 90 percent maximum carapace width; eyestalks well-calcified; protogastric, hepatic, and cardiac regions with prominent transverse ridges; sternal sutures 4/5, 5/6, and 6/7 incomplete, pleonal locking mechanism on sternite 5, sternite 8 visible in ventral view; all male pleonal somites free, somites 2, 3, and 4 with transverse keels; chelipeds keeled and spined; fifth pereiopods with paddle-like propodi and dactyli. [Emended from SCHWEITZER, FELDMANN, & KARASAWA, 2007.] *Lower–Upper Cretaceous* (*Albian–Cenomanian*): USA (Texas). *Upper Cretaceous* (*Turonian–Maastrichtian*). *Turonian*: Colombia. *Campanian*: Morocco. *Maastrichtian*: Brazil, Colombia, Venezuela, USA (Alabama, Mississippi, South Carolina, Texas).—FIG. 5, 4a–b. **O. stephensoni*, Maastrichtian, Texas, USA, *a*, paratype UT 21258, dorsal carapace; *b*, UT 21262, ventral surface, scale bars, 1 cm (Schweitzer, Feldmann, & Karasawa, 2007, fig. 1C, 1G).
- Parathranites** MIERS, 1886, p. 185 [**Lupocyclus* (*Parathranites*) *orientalis*, p. 186, pl. 17, 1; M (ICZN Opinion 73, 1922, p. 27)]. Carapace wider than long; front with four spines including inner-orbital spines; orbits with two fissures; anterolateral margins with five spines including outer-orbital spines, last spine longest and extending laterally; posterolateral margin short; posterolateral corner with large blunt protuberance; posterior margin weakly convex; carapace regions moderately well defined, ornamented with a few large tubercles. *Miocene–Holocene*. *Miocene* (*Burdigalian*): Japan. *Holocene*: Indo-West Pacific Ocean, Hawaii.—FIG. 6, 1. *Parathranites shibatai* KARASAWA, 1990, holotype MFM 9032, Burdigalian, Japan, scale bar, 1 cm (new).
- Pleolobites** REMY, 1960, p. 59 [**P. erinaceus*, p. 59, plate-fig. 10–11; OD]. Carapace wider than long, length about 75 percent maximum width; front with four blunt spines including inner-orbital spines; orbits deep, with one fissure and notch, fronto-orbital width about half maximum carapace width; anterolateral margins with five spines including outer-orbital spines, second and third spines broadly triangular, fourth spine situated nearly on base of fifth, very long, laterally directed spine; posterolateral margins slightly convex; posterior margin nearly straight; protogastric, hepatic, epibranchial, and branchial regions with large tubercles centrally. *Eocene*: Ivory Coast.—FIG. 6, 2a–b. **P. erinaceus*, holotype MNHN FR03782, dorsal (*a*) and ventral (*b*) surfaces, scale bars, 1 cm (photo by J. Falconnet, Project Reclonat, MNHN).
- Polybius** LEACH, 1820 in 1815–1875, pl. 9B [**P. henslowi*; M]. Carapace not much wider than long, front with three spines including inner orbital spines. *Holocene*: North Atlantic Ocean, Mediterranean Sea.—FIG. 6, 3a–b. **P. henslowi*, USNM 112978, Holocene, North Atlantic Ocean, dorsal (*a*) and ventral (*b*) surfaces; scale bars, 1 cm (new).
- Pororaria** GLAESSNER, 1980, p. 187 [**P. eocenica*, p. 187, fig. 15–16; OD]. Carapace about as long as wide; front with four lobes including inner-orbital; orbits with two fissures; outer-orbital spine projected forward; anterolateral margins with five spines, last spine smallest; posterolateral margins straight; posterior margin concave axially; regions well defined; epibranchial region arcuate; sternite 3 with lateral swellings; sternite 4 long, with swellings parallel to lateral margins; sternal sutures 4/5

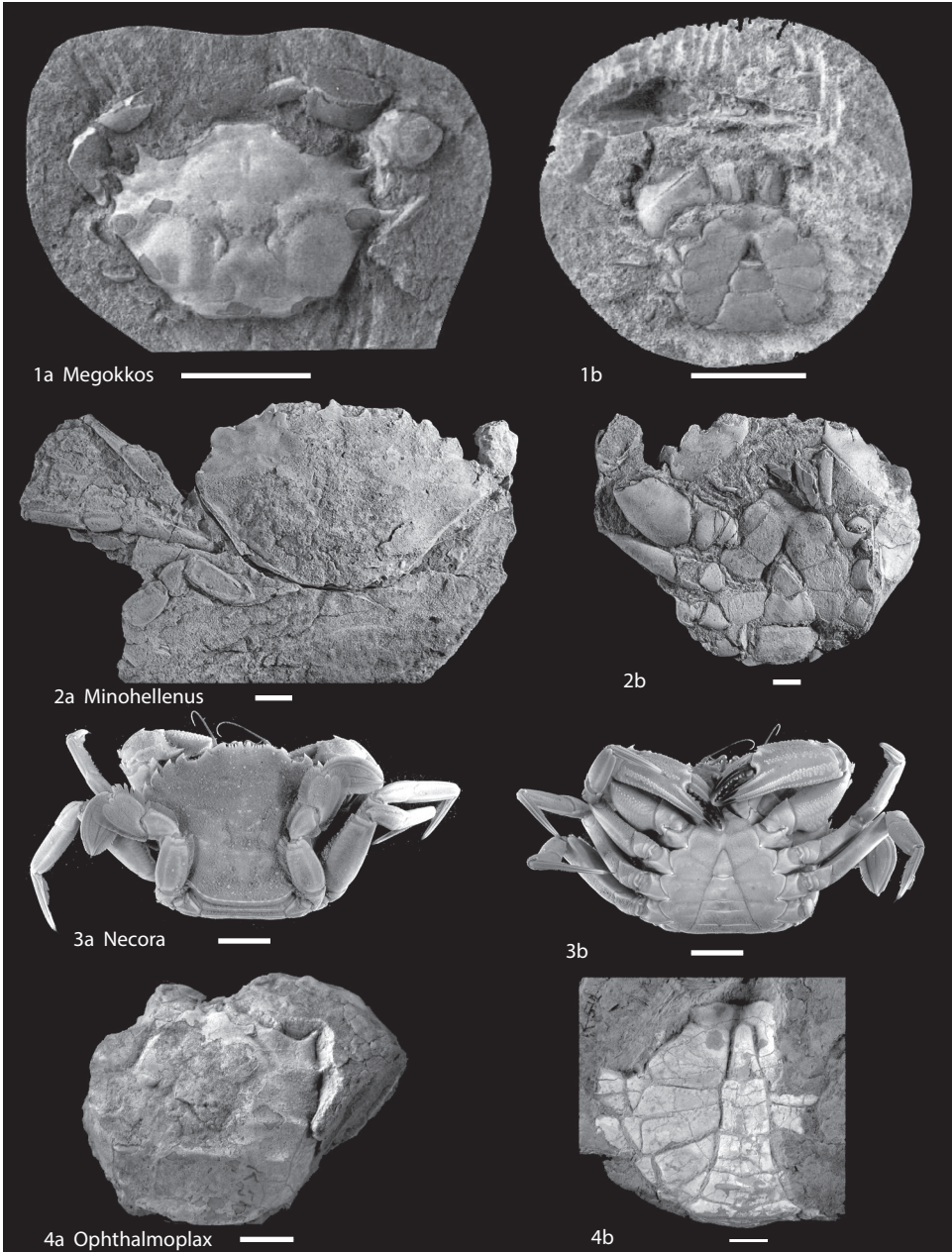


FIG 5. Carcinidae (p. 9–11).

and 5/6 incomplete; chelipeds isochelous, mani with rows of small spines on outer surface. *Eocene* (Bartonian–Priabonian): New Zealand.—FIG. 6, 4a–b. **P. eocenica*; a, NZGS AR 929, dorsal view; b, NZGS AR 930, anterior ventral view; scale bars,

1 cm (Feldmann & Maxwell, 1990, fig. 11,6 and 11,2, respectively). **Portufuria** COLLINS, SCHULZ, & JAKOBSEN, 2005, p. 20 [*P. enigmatica*, p. 20, pl. 1,3; OD]. Carapace hexagonal, not much wider than long; front with

three spines including inner-orbital spines; outer-orbital spine long; fronto-orbital width about half maximum carapace width; anterolateral margin with four spines; chelipeds weakly heterochelate.

Eocene (Ypresian): Denmark.—FIG. 7, 1. **P. enigmatica*, holotype MGUH 27742, scale bar, 1 cm (Collins, Schulz, & Jakobsen, 2005, pl. 1, 3A).

Portunites BELL, 1858, p. 20 [**P. incertus*, p. 20, pl. 3, 1–5; M] [= *Leiocbilus* REUSS, 1859, p. 56 (type, *L. morrissi*, p. 56, pl. 18, 7, M)]. Carapace wider than long, widest at position of last anterolateral spine; ovate-hexagonal in shape; carapace regions inflated, well defined, delimited by broad grooves; front not projected beyond orbits, with six lobes or small, blunt spines including inner orbital spines; orbits circular, two fissures; anterolateral margin with five spines including outer-orbital spine, second spine smallest and sometimes absent, last spine usually longest; brachial region with longitudinal ridge parallel to and on either side of longitudinal axis of cardiac region, ridge usually with tubercles at either end. *Eocene–Miocene. Eocene (Ypresian)*: Italy, Tunisia, UK (England). *Eocene (Lutetian)*: UK (England). *Eocene (Priabonian)*: USA (Washington). *Eocene*: Hungary, Japan, Oregon, USA (Washington). *Miocene*: Germany.—FIG. 7, 2. **P. incertus*, NHMUK In. 63046, Lutetian, UK (England), scale bar, 1 cm (new).

Rhachiosoma WOODWARD, 1871, p. 91 [**R. bispinosa*, p. 91, pl. 4, 3; SD GLAESSNER, 1929, p. 372]. Carapace wider than long, ovate; front with six spines including inner-orbital spines; orbits small, with two fissures; fronto-orbital width about half maximum carapace width; anterolateral margins with four spines including outer-orbital spine, increasing in size posteriorly to very long, laterally directed last spine which extends onto dorsal carapace into weakly arcuate epibranchial region; protogastric and epibranchial regions with large tubercles; brachial regions with oblique ridge of three tubercles subparallel to axis. *Eocene (Ypresian)*: UK (England).—FIG. 7, 3a–b. **R. bispinosa*, NHMUK 59223, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Subfamily THIINAE Dana, 1852

[*nom. transl.* ALCOCK, 1899, p. 5 ex Thiidae DANA, 1852, p. 86] [= Nautilocorystidae ORTMANN, 1893, p. 28]

Carapace about as long as wide, widest in anterior third to half, smooth overall; front projected weakly beyond orbits, with even number of spines or lobes or entire; orbits small, shallow, directed forward, with one fissure; anterior margin extending some distance laterally from orbits to make wide anterior margin; lateral margins nearly parallel anteriorly, curving convexly and converging posteriorly; lateral margins with

four or five lobes or spines; posterior margin narrow, about as wide as front, posterolateral reentrant absent; chelipeds short, barely extending beyond anterior margin of carapace; pereopods 4 and 5 with ovate mani and lanceolate dactyls; sternal sutures 4/5 through 7/8 incomplete; male pleon with somites free; male gonopods 1 and 2 short. [Emended from DAVIE, GUINOT, & NG, 2015, p. 1103.] *Pliocene–Holocene*.

Thia LEACH 1816 (imprint 1815), p. 312 [**T. polita*; M; = *Hippa scutellata* FABRICIUS, 1793, p. 474; = *Cancer residuus* HERBST, 1799 in 1782–1804, p. 53, pl. 48, 1; = *Thia blainvillii* RISSO, 1822, p. 241]. As for family. *Pliocene–Holocene. Pliocene*: Fiji. *Holocene*: Northeast Atlantic Ocean, Mediterranean Sea.—FIG. 7, 4a–b. **T. scutellata* (FABRICIUS) USNM 258286, Holocene, Spain, dorsal (a) and ventral (b) views; scale bars, 1 cm (new).

Family GERYONIDAE Colosi, 1924

[Geryonidae COLOSI, 1924, p. 249]

Carapace ovate to hexagonal, wider than long, smooth to granular, regions weakly or moderately defined, often with arcuate ridge on epibranchial area; front with even number of spines and axial notch or rarely with three spines; orbits only moderately wide, with one or two fissures which may be indistinct, inner orbital angle defined by a node or spine, lower orbital tooth long, visible dorsally; anterolateral margin convex with three to five spines; suture delimiting sternites 3 and 4 well marked, sternal sutures usually 4/5 and 5/6 incomplete, 6/7 barely incomplete, 7/8 complete; sternite 8 not visible ventrally but a small portion visible in posterior view; posterior prolongation of male episternite 7 not marked; pleon with seven somites visible in males and females but somites 3–5 immovable in males, somites 2–3 or 1–3 with transverse keel; telson of male pleon reaches posterior of sternite 4; chelipeds unequal, shorter than pereopods, with distal, inner spine on carpus; pereopod 5 with ovate propodus, dactylus ovate or lanceolate. [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 96; EVANS, 2018, p. 39.] *Oligocene (Chattian)–Holocene*.

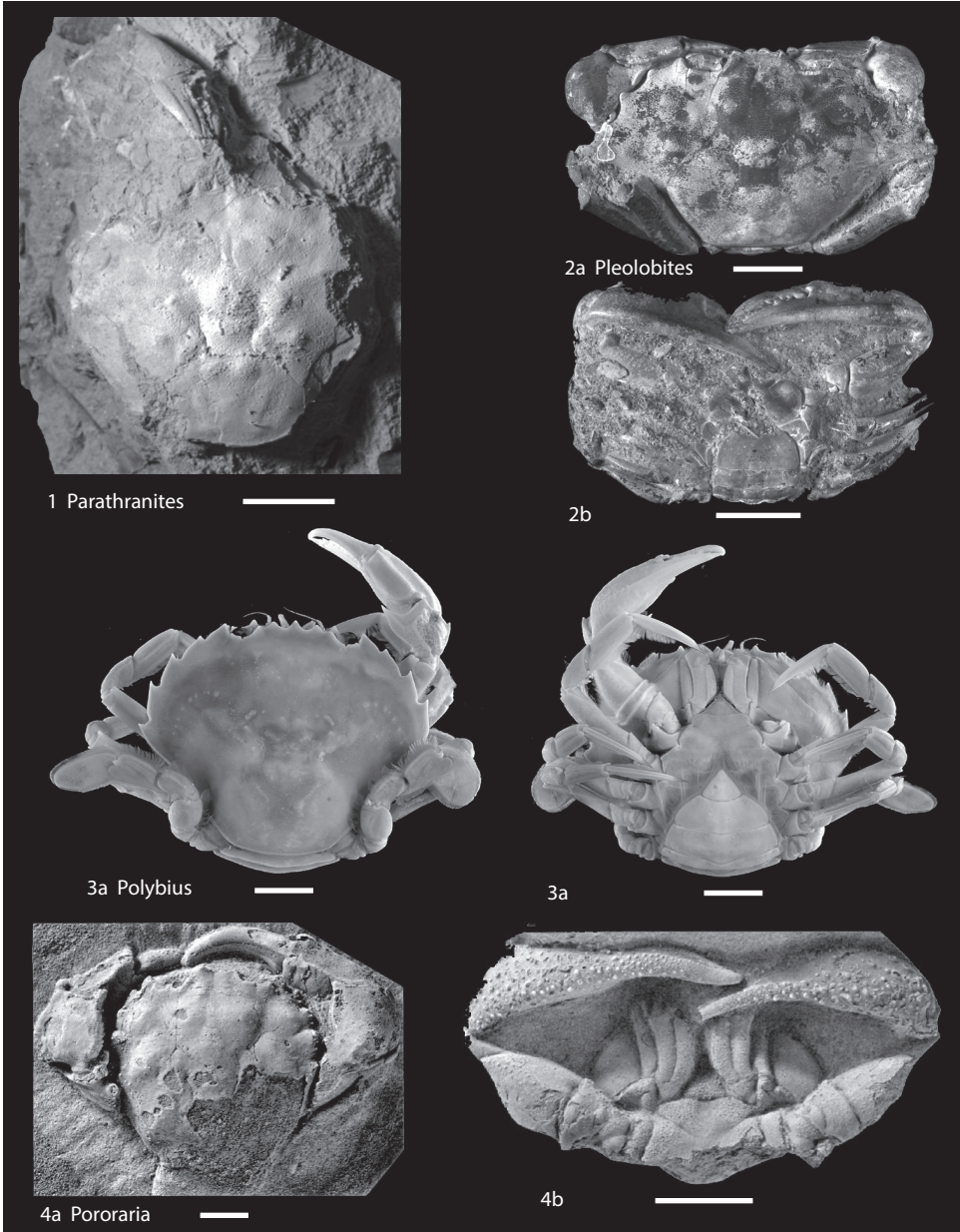


FIG 6. Carcinidae (p. 11–12).

Subfamily GERYONINAE Colosi, 1924

[*nom. transl.* ŠTEVČIČ, 2005, p. 63 *ex* Geryonidae COLOSI, 1924, p. 249]

Carapace hexagonal, wider than long, smooth to granular, regions weakly or moderately defined, often with arcuate

ridge on epibranchial area; front with even number of spines and axial notch; orbits only moderately wide, with one or two indistinct fissures, inner orbital angle defined by a node or spine, lower orbital tooth long, visible dorsally; anterolateral margin convex

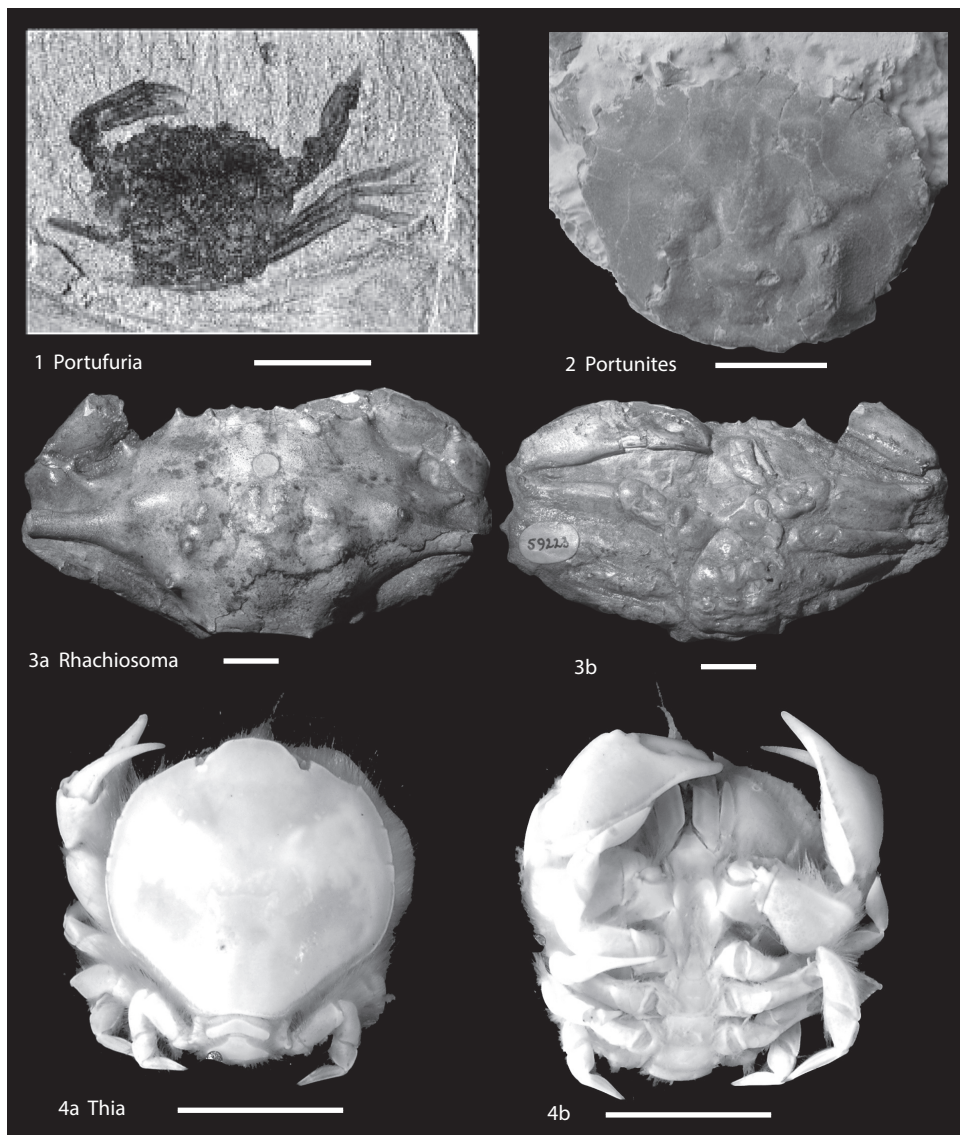


FIG 7. Carcinidae (p. 12–13).

with three to five spines; suture delimiting sternites 3 and 4 well marked, sternal sutures 4/5 and 5/6 incomplete, 6/7 and 7/8 nearly complete; sternite 8 not visible ventrally but a small portion visible in posterior view; posterior prolongation of male episternite 7 not marked; pleon with seven somites visible in males and females but somites 3–5 immovable in males, somites 2–3 or

1–3 with transverse keel, somite 3 usually widest; telson of male pleon reaches posterior of sternite 4; chelipeds unequal, shorter than pereopods, with distal, inner spine on carpus; pereopod 5 with ovate propodus, dactylus ovate or lanceolate. [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 96; EVANS, 2018, p. 39.] *Oligocene (Chat-tian)–Holocene.*

- Geryon KRØYER, 1837, p. 10 [**G. tridens*; M (ICZN Opinion 85, 1925, p. 15); =*Cancer tridens* HERBST, 1790 in 1782–1804, p. 267, pl. 21, 125 (suppressed by ICZN, Opinion 712, 1964, p. 336); =*Cancer tridens* FABRICIUS, 1798, p. 340 (homonym of *C. tridens* HERBST, ICZN Opinion 712, 1964, p. 344)] [= *Chalaepeus* GERSTAECKER, 1856, p. 118 (type, *Cancer trispinosus* HERBST, 1803, in 1782–1804, p. 43, pl. 57, 4, M)]. Anterolateral margins with three spines; frontal spines small. *Pliocene–Holocene*. *Pliocene*: Chile. *Holocene*: north Atlantic Ocean, Mediterranean Sea, South Africa.—FIG. 8, 1a–b. **G. tridens*, USNM 210931, Holocene, The Netherlands, dorsal (a) and ventral (b) surfaces; scale bars, 1 cm (new).
- Archaeoplax STIMPSON, 1863, p. 584 [**A. signifera*; p. 584, pl. 12; M]. Carapace rectangular; front with front lobes; orbits long, upper orbital margin sinuous, outer-orbital spine short; anterolateral margins short, with four spines including outer-orbital spine; posterolateral margins long, straight; posterolateral reentrant large; posterior margin concave; branchial regions with longitudinal ridges. *Miocene*: USA (Massachusetts).—FIG. 8, 2a–b. **A. signifera*, USNM MO 371430A; dorsal (a) and ventral (b) surfaces; scale bars, 1 cm (new).
- Chaceon MANNING & HOLTHUIS, 1989, p. 51 [**Geryon fenneri* MANNING & HOLTHUIS, 1984, p. 666; OD]. Frontal margin with four spines long, well developed; anterolateral margins with five spines including outer-orbital spine; carapace regions moderately developed; pereiopods 2–5 long, slender. *Oligocene–Holocene*. *Oligocene* (*Chat-tian*): Austria. *Oligocene*: Argentina, Germany, Peru. *Miocene*: Argentina, Chile, Denmark, Peru. *Pliocene–Pleistocene*: Japan. *Holocene*: Cosmopolitan.—FIG. 8, 3a–b. *Chaceon peruvianus* (D'ORBIGNY, 1842), NHMUK In. 28002, Miocene, Argentina, dorsal (a) and ventral (b) surfaces; scale bars, 1 cm (Schweitzer & Feldmann, 2000, fig. 9.1, 9.3; photos by P. Hurst).

**Subfamily OVALIPINAE Spiridinov,
Neretina, & Schepetov, 2014**

[*nom. transl.* EVANS, 2018, p. 28 ex Ovalipidae SPIRIDINOV, NERETINA, & SCHEPETOV, 2014, p. 420]

Carapace ovate, wider than long, smooth, regions weakly or moderately defined, typically with arcuate ridge on epibranchial area; front with three or four spines; orbits only moderately wide, with one or two fissures, inner orbital angle defined by a node or spine, lower orbital tooth long, visible dorsally; anterolateral margin convex, with five spines; suture delimiting sternites 3 and 4 well marked, sternal sutures 4/5 and 5/6 complete, 6/7 incomplete; 7/8 complete; sternite 8 not visible ventrally but a small

portion visible in posterior view; posterior prolongation of male episternite 7 not marked; pleon with seven somites visible in males and females but somites 3–5 immovable in males, somites 2–3 or 1–3 with transverse keel, somite 3 usually widest; telson of male pleon reaches posterior of sternite 4; chelipeds unequal, shorter than pereopods, with distal, inner spine on carpus; pereiopod 5 with ovate propodus, dactylus ovate or lanceolate. [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 96; EVANS, 2018, p. 39.] *Pliocene–Holocene*.

Ovalipes RATHBUN, 1898, p. 597 [**Cancer ocellatus* HERBST, 1799 in 1782–1804, p. 61; OD] [= *Anisopus* DE HAAN, 1833 in 1833–1850, p. 12 (type, *Corystes (Anisopus) punctata*, SD RATHBUN, 1930, p. 18, non *Anisopus* MEIGEN, 1803, p. 264); = *Aeneacancer* WARD, 1933, p. 381 (type, *A. mollerii*, OD)]. Carapace slightly wider than long; front with three or four spines including inner orbital spines, not projecting beyond orbits; orbits closely spaced, directed forward, with one orbital fissure and sometimes with intra-orbital spine; anterolateral margin with five spines including outer-orbital spines; posterolateral margin concave; posterolateral corner with large, blunt protuberance; posterior margin sinuous, concave laterally and convex centrally; regions poorly defined; branchiocardiac grooves deep lateral to cardiac region. *Pliocene–Holocene*. *Pliocene*: Japan, New Zealand. *Pleistocene*: Japan, New Zealand, Taiwan, USA (Florida). *Holocene*: Cosmopolitan antitropical.—FIG. 8, 4a–b. **O. ocellatus* (HERBST), USNM 4894, Holocene, Massachusetts, USA, dorsal (a) and ventral (b) surfaces, scale bars, 1 cm (new).

**Family LITHOPHYLACIDAE
Van Straelen, 1936**

[Lithophylacidae VAN STRAELEN, 1936, p. 43] [= *Leiocarcininae* ŠTEVČIČ, 2005, p. 69]

Carapace hexagonal, wider than long, widest about one-third the distance posteriorly; rostrum very narrow; orbits extremely wide, occupying entire maximum width of carapace, angling obliquely posteriorly and terminating in anterolaterally directed outer-orbital spine; lateral margins converging posteriorly, with one projection at epibranchial region; posterior margin very wide; carapace regions well defined; sternal suture 4/5 interrupted, sutures 5/6 through 7/8 presumably complete; sternite 8 not visible in ventral view; male pleon with all somites

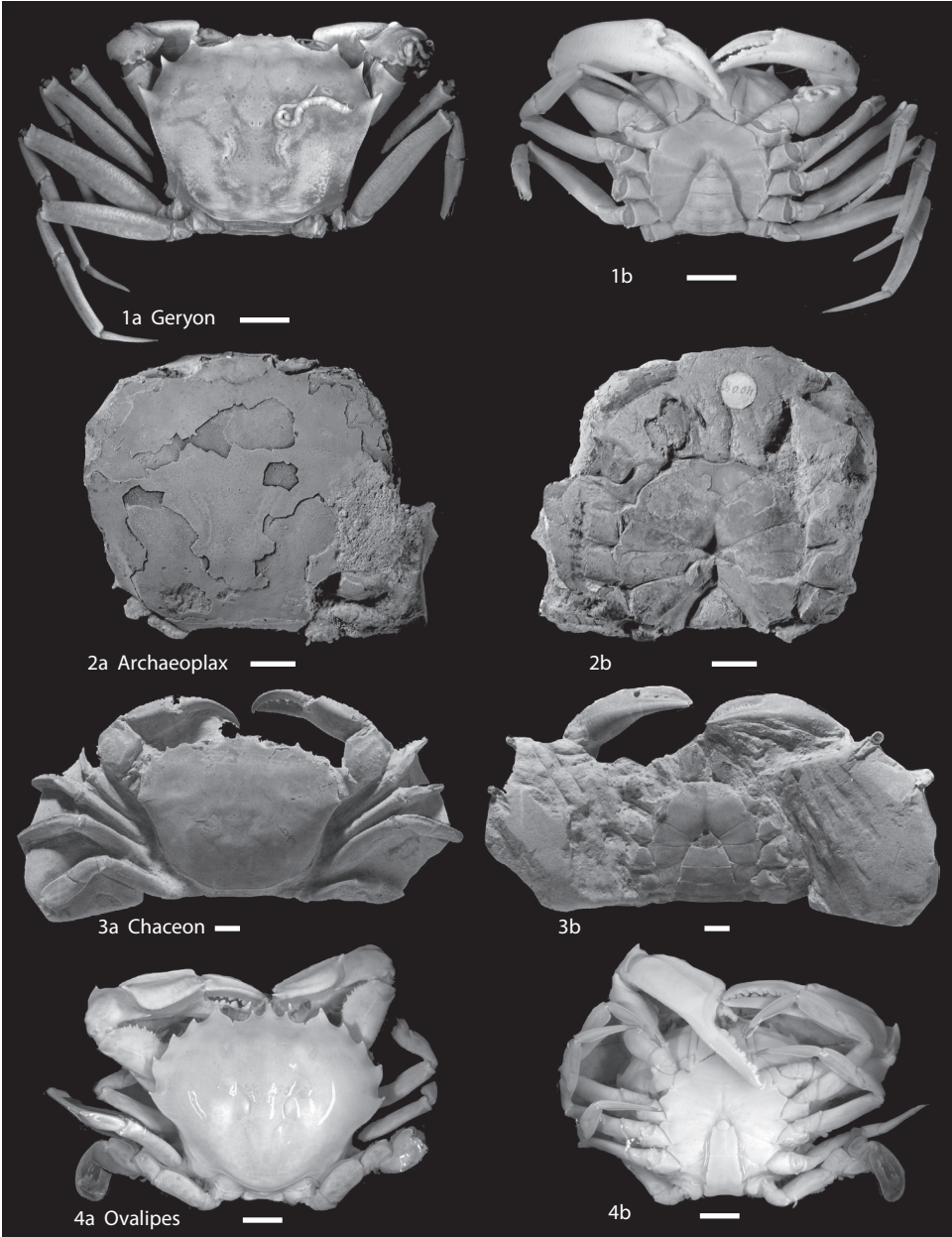


FIG 8. Geryonidae (p. 16).

free, pleonal somite 3 with transverse keel; pleonal press-button mechanism present; stridulatory devices present on carapace margin just posterior to outer-orbital spine. [Emended from GUINOT & BRETON, 2006,

p. 600.] *Upper Cretaceous (Cenomanian)–Paleocene (Danian)*.

Lithophylax A. MILNE-EDWARDS & BROCCHI, 1879, p. 116 [**L. trigeri*; p. 117; M]. Carapace hexagonal, wider than long, widest about one-third

the distance posteriorly; rostrum very narrow; orbits extremely wide, occupying entire maximum width of carapace, angling obliquely posteriorly and terminating in anterolaterally directed outer-orbital spine; lateral margins converging posteriorly, with one projection at epibranchial region; posterior margin very wide; carapace regions well defined; sternal suture 4/5 interrupted, sutures 5/6 through 7/8 presumably complete; sternite 8 not visible in ventral view; male pleon with all somites free, pleonal somite 3 with transverse keel; pleonal press-button mechanism present; stridulatory devices present on carapace margin just posterior to outer-orbital spine. *Upper Cretaceous (Cenomanian–Maastrichtian)*. *Cenomanian*: France. *Maastrichtian*: USA (Mississippi, New Jersey, Tennessee).—FIG. 9,1. **L. trigeri*, BSP 1988 III 196, Cenomanian, France, scale bar, 1 cm (Schweitzer, Feldmann, & Karasawa, 2007, fig. 3G).

Branchiocarcinus VEGA, FELDMANN, & SOUR-TOVAR, 1995, p. 344 [**B. cornatus*, p. 345, fig. 5; OD]. Carapace hexagonal to trapezoidal, slightly wider than long, widest anteriorly; anterolateral margins curved, with two anteriorly curved, sharp spines; posterolateral margins straight, posteriorly convergent; posterior margin weakly concave; epi-, meso-, and metabranchial regions with oblique or transverse ridges, branchial regions large; cervical groove deep. *Upper Cretaceous (Maastrichtian)*: Mexico (San Luis Potosi).—FIG. 9,2. **B. cornatus*, holotype IGM 6244, scale bar, 1 cm (Vega, Feldmann, & Sour-Tovar, 1995, fig. 5).

Icriocarcinus BISHOP, 1988, p. 247 [**I. xestos*, p. 247, fig. 2–3; OD]. Carapace wider than long; regions defined by deep grooves; epibranchial region forming well-defined arcuate ridge defined by deep grooves; front long, extremely narrow, widening slightly distally; fronto-orbital width occupying maximum carapace width; orbits sloping obliquely and posteriorly; two intra-orbital spines; male pleon; filling entire space between coxae of fifth pereopods; somite 3 widest of all somites, with transverse keel. *Upper Cretaceous–Paleocene*. *Upper Cretaceous (Campanian–Maastrichtian)*: Mexico (Baja California), USA (California). *Maastrichtian*: Mexico (Chiapas). *Paleocene (Danian)*: USA (California).—FIG. 9,3. **I. xestos*, holotype SDSNH 26038, Campanian–Maastrichtian, California, USA, scale bar, 1 cm (Schweitzer, Feldmann, & Karasawa, 2007, fig. 3A).

Icriobranchiocarcinus VEGA in VEGA, CHARBONNIER, GÓMEZ-PÉREZ, COUTIÑO, CARBOT-CHANONA, TÁVORA, SERRANO-SÁNCHEZ, TÉODORI, & HERNÁNDEZ-MONZÓN, 2018, p. 335 [**I. tzutzuz*; OD]. Carapace with several transverse ridges on branchial and hepatic regions, outer orbital angle strongly produced. *Upper Cretaceous (Maastrichtian)*: Cuba, Mexico.—FIG. 9,4a–b. *Icriobranchiocarcinus* sp., IGM 11515, Maastrichtian, Cuba, dorsal (a) and ventral (b) views, scale bars 1 cm (new; photo by F. J. Vega, UNAM).

Family LONGUSORBIIDAE Karasawa, Schweitzer, & Feldmann, 2008

[Longusorbiidae KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 95]

Carapace wider than long, maximum length ranging from 70 to 80 percent maximum width, widest at position of hepatic region, posterior to outer-orbital angle, about 30 percent the distance posteriorly; lateral margins of carapace converging posteriorly; front interpreted to lie between interiormost orbital notches, axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly downturned distally so that distal part is nearly perpendicular to dorsal carapace; frontal width about 40 percent maximum carapace width; orbits extremely broad, sinuous, with notches, spines, or blunt protuberances; orbits angling posteriorly; eyestalks appear to be well calcified; fronto-orbital width about equal to maximum carapace width; mesogastric region merging with rostral sulcus; gastric regions short; branchial regions long; urogastric region about as wide as mesogastric and cardiac regions; epibranchial region arcuate; metabranchial region with inflated oblique ridge parallel to margin; carapace surface with tubercles; sternum relatively narrow compared to other portunoids, about as long as wide, sternites 1/2 fused, no evidence of suture; sternal suture 2/3 entire; sternal suture 3/4 expressed as a marginal notch and weak groove, well marked; sternite 4 long; sternal sutures 4/5 and 5/6 not parallel; sternal suture 4/5 at high angle; sternite 8 not visible in ventral view; male pleon extending to about middle of sternite 4 and about middle of coxae of pereopods 1; all male pleonal somites free, entirely filling space between coxae of fifth pereopods; chelae stout, markedly heterochelate, shorter than pereopods; fingers with black tips; meri and carpi of fourth and fifth pereopods flattened; propodi of fourth and fifth pereopods elliptic; dactylus of fifth pereopod narrow, lanceolate. [SCHWEITZER, FELDMANN, & KARASAWA, 2007, p. 29.] *Upper Cretaceous (Cenomanian)–Eocene*.

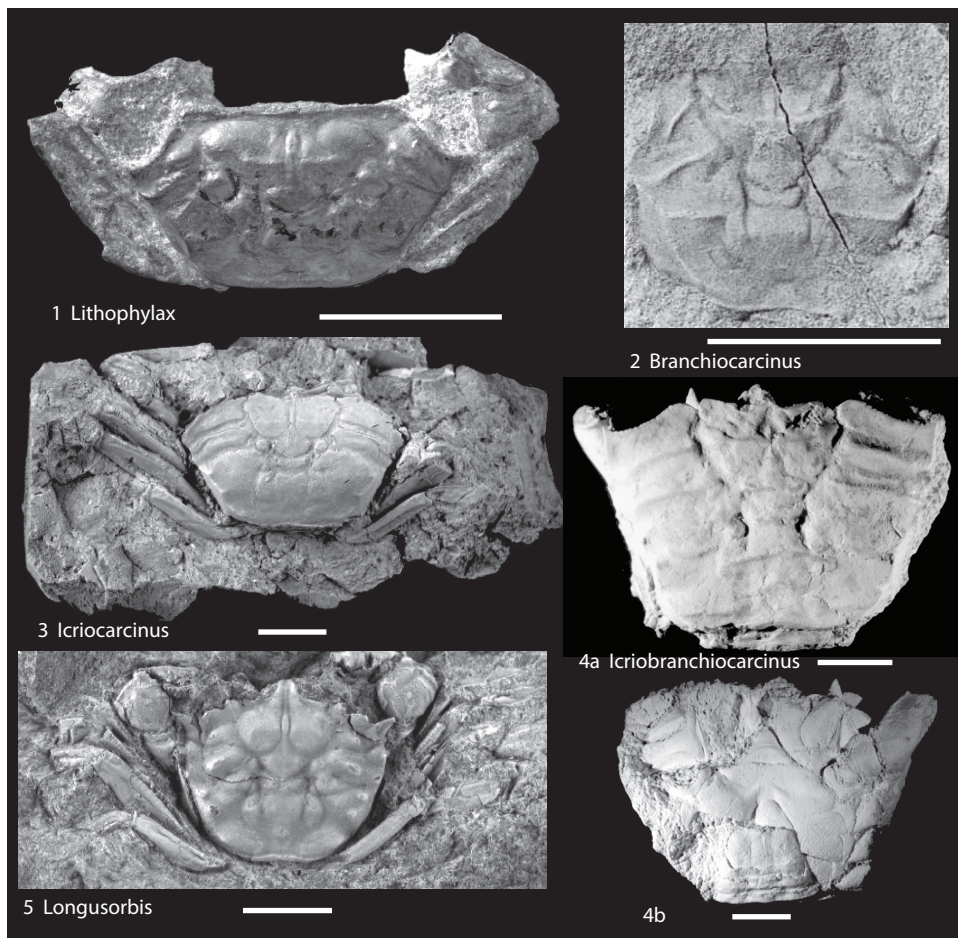


FIG 9. Lithophylacidae, Longusorbiidae (p. 17–20).

Longusorbis RICHARDS, 1975, p. 1857 [**L. cuniculosus*, p. 1858, fig. 4–5, 7–12; OD]. Carapace wider than long, maximum length ranging from 70 to 80 percent maximum width, widest at position of hepatic region, posterior to outer-orbital angle, about 30 percent the distance posteriorly; lateral margins of carapace converging posteriorly; front interpreted to lie between interior-most orbital notches, axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly downturned distally so that distal part is nearly perpendicular to dorsal carapace; frontal width about 40 percent maximum carapace width; orbits extremely broad, sinuous, with notches, spines, or blunt protuberances; orbits angling posteriorly; eyestalks appear to be well calcified; fronto-orbital width about equal to maximum carapace width; mesogastric region merging with rostral sulcus; gastric regions short; branchial regions

long; urogastric region about as wide as mesogastric and cardiac regions; epibranchial region arcuate; metabranchial region with inflated oblique ridge parallel to margin; carapace surface with tubercles; sternum relatively narrow compared to other portunoids, about as long as wide, sternites 1/2 fused, no evidence of suture; sternal suture 2/3 entire; sternal suture 3/4 expressed as a marginal notch and weak groove, well marked; sternite 4 long; sternal sutures 4/5 and 5/6 not parallel; sternal suture 4/5 at high angle; sternite 8 not visible in ventral view; male pleon extending to about middle of sternite 4 and about middle of coxae of pereopods 1; all male pleonal somites free, entirely filling space between coxae of fifth pereopods; chelae stout, markedly heterochelate, shorter than pereopods; fingers with black tips; meri and carpi of fourth and fifth pereopods flattened; propodi of fourth and fifth pereopods elliptic; dactylus of

fifth pereopod narrow, lanceolate. [SCHWEITZER, FELDMANN, & KARASAWA, 2007, p. 29.] *Upper Cretaceous–Eocene. Upper Cretaceous (Cenomanian, Coniacian)*: Mexico (Guerrero). *Campanian*: Canada (British Columbia). *Eocene*: Mexico (Baja California Sur).—FIG. 9.5. **L. cuniculosus*, KSU D 746, Campanian, British Columbia, Canada, scale bar, 1 cm (Schweitzer, Feldmann, & Karasawa, 2007, fig. 2A).

Family PORTUNIDAE Rafinesque, 1815

[*nom. correct.* SAMOUELLE, 1819, p. 83 *pro* Portunidia RAFINESQUE, 1815, p. 97] [=Archaeoportunidae ARTAL, OSSÓ, & DOMÍNGUEZ, 2013, p. 309]

Carapace wider than long, often markedly so; commonly ornamented with an arcuate epibranchial keel; anterolateral margin with three to nine spines including outer-orbital spine; orbits usually with two fissures; orbits generally moderate in size but can be very wide, directed forward or slightly anterolaterally; fronto-orbital width ranging from about half the maximum carapace width to the entire carapace width; sternum usually wide, ovate; secondary sulcus delimits sternites 6 and 7; median transverse ridge between sternite 6 and 7 present; median line on thoracic sternites up to sternite 6; sternite 8 clearly visible in ventral view, often markedly so; male pleon with somites 3–5 fused, weak remnants of sutures may remain, somite 3 markedly wider than other somites, somite 3 with transverse keel; lobe on endopodite of first maxilliped present (portunid lobe); chelipeds longer than other pereopods; chela often with keels but may be smooth; fifth pereopod with paddle-like dactyls and usually with ovate propodi; male first gonopod with or without subterminal spines (KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 103). *Eocene (Ypresian)–Holocene.*

Enoplnotus A. MILNE-EDWARDS, 1860, p. 246 [**E. armatus*, p. 247; M]. Carapace much wider than long, branchiocardiac depressions very deep; anterolateral margins with many spines, last spine very long, extending laterally, ornamented with several small spines on upper surface; carapace surface with scattered tubercles and possibly a row of tubercles paralleling anterolateral margin. *Eocene*: Italy.—FIG. 10.1. **E. armatus*, scale unknown (A. Milne-Edwards, 1860, pl. 7, 1).

Archaeoportunus ARTAL, OSSÓ, & DOMÍNGUEZ, 2013, p. 309 [**A. isabensis*, p. 309, fig. 3–5; OD].

Carapace wider than long, widest at position of last anterolateral spine, over half the distance posteriorly; front with four spines; anterolateral margins with nine spines including outer orbital, last spine much the longest, directed posterolaterally; protogastric, hepatic, mesogastric, cardiac, and epibranchial regions with sharp transverse keels; sternum narrow for superfamily, sternite 8 in males not visible; male pleonal somites may be fused but with clear sutures. *Eocene (Ypresian)*: Spain.—FIG. 10.2a–b. **A. isabensis*, holotype, MGSB 68576, dorsal (a) and ventral (b) views, scale bars, 1 cm (new; photo by À. Ossó, Tarragona, Spain).

Subfamily CARUPINAE Paulson, 1875

[Carupinae PAULSON, 1875, p. 69] [=Atoportunini ŠTEVČIČ, 2005, p. 86; =Catoptrinae BORRADAILE, 1903, p. 427; =Goniocaphyrinae BORRADAILE, 1900, p. 577; =Kumini ŠTEVČIČ, 2013, p. 187; =Libystinae ŠTEVČIČ, 2005, p. 87; =Pelini ŠTEVČIČ, 2011, p. 131; =Richerellini ŠTEVČIČ, 2011, p. 132]

Carapace transversely ovate, generally smooth, wider than long, length about 60–75 percent maximum width, position of maximum width variable; front lobate, with two to six lobes including inner-orbital lobes or entire, occupying about 30–35 percent maximum carapace width; orbits forward directed, with one or two orbital fissures or fissures absent, fronto-orbital width variable, 25–70 percent maximum carapace width; anterolateral margins with four to nine spines including outer-orbital spines or entire; posterolateral reentrants large; basal antennal article much longer than wide, without laterodistal spine; antennal flagellum within orbit; chelipeds longer than other pereopods and stouter, chelae smooth or with weak keels; sternite 8 visible in ventral view, sternal sutures 4/5, 5/6, and 7/8 discontinuous, 6/7 discontinuous or continuous; male pleonal somites 2–5 or 3–5 fused, sutures not evident; pereopod five with ovate, obovate, or lanceolate propodi and dactyl; first male gonopod stout. [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 97, 103–104.] *Eocene (Ypresian), Miocene–Holocene.*

Carupa DANA, 1851, p. 129 [**C. tenuipes* DANA, 1852, p. 85; M (ICZN Opinion 73, 1922, p. 26); =*C. laeviuscula* HELLER, 1862, p. 520]. Carapace transversely oval, much wider than long; front with four obtuse lobes; upper orbital margin with two fissures; anterolateral margin with seven spines; dorsal surface convex, smooth, with poorly defined

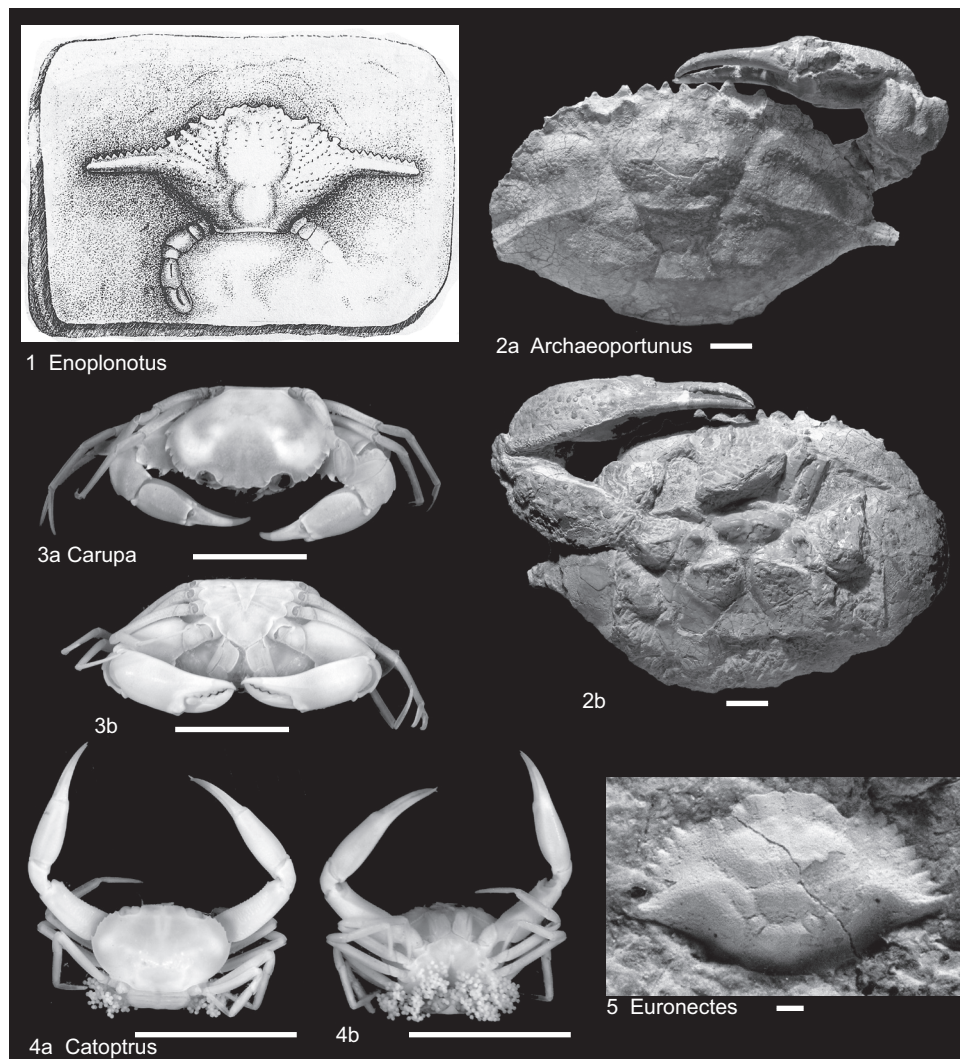


FIG 10. Portunidae (p. 20–22).

regions; chelipeds subequal; dactyli of pereopods five paddle shaped. *Miocene–Holocene*: *Miocene* (Langbian): Hungary. *Miocene*: Taiwan. *Pleistocene*: Taiwan. *Holocene*: Indo-Pacific Ocean, Red Sea, east Africa.—FIG. 10, 3a–b. **C. laeviuscula*, USNM 153943, Holocene, Solomon Islands, oblique anterior (a) and oblique ventral (b) views, scale bars, 1 cm (new).

Catoptrus A. MILNE-EDWARDS, 1870, p. 1 [**C. nitidus*; M (ICZN Opinion 85, 1925, p. 14)] [= *Goniocaphyra* DE MAN, 1888, p. 339, pl. 14, 1 (type, *G. truncatifrons*, M)]. Carapace transversely oval; front bilobed; anterolateral margins with six small spines including outer-orbital spines; posterolateral margins convex; posterolateral reentrant

well defined; chelipeds stout, other pereopods slender. *Holocene*: Australia, Indo-Pacific Ocean, Red Sea.—FIG. 10, 4a–b. *C. inaequalis* (RATHBUN, 1906), USNM 29661, Holocene, Hawaii, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Euronectes KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 103 [**Rakosia grumiensis* BESCHIN, DE ANGELI, & CHECCHI, 2001, p. 23, pl. 2, 3, 6; OD]. Carapace wider than long, length about 64 percent maximum width, widest at about 65 percent maximum carapace length; front with six blunt lobes including inner-orbital lobes, about one-quarter to one-third carapace width; orbits appearing to have been fairly shallow, with broad rim, fronto-orbital width about 60 percent

- maximum carapace width; anterolateral margin longer than posterolateral margin, with nine short, triangular spines including outer-orbital spine, last spine longest, more attenuated than other spines; posterolateral margin concave; posterior margin nearly straight, rimmed; protogastric regions with very weak transverse keel; epibranchial ridge strongly arched anteriorly; axial regions well marked; pterygostomial region may have stridulating ridges (KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 103). *Oligocene–Miocene. Oligocene (Rupelian)*: Italy. *Miocene (Langhian)*: Spain.—FIG. 10, 5. **E. grumiensis* (BESCHIN, DE ANGELI, & CHECCHI), MCZ 2128, Oligocene, Italy, scale bar, 1 cm (new; photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).
- Laleonectes** MANNING & CHACE, 1990, p. 50 [**Neptunus vocans* A. MILNE-EDWARDS, 1878, p. 225; OD]. Carapace wider than long, hexagonal, length about 80 percent maximum width; front with six spines; orbits rimmed; anterolateral margins with nine spines including small outer-orbital spine, last spine longest; carapace regions moderately defined as swellings and with smaller swellings on them; chelipeds stout, pereopods 2–4 very slender, pereopod 5 with ovate manus and dactylus. *Pleistocene–Holocene. Pleistocene*: Barbados, Jamaica. *Holocene*: Cosmopolitan tropical.—FIG. 11, 1a–b. **L. vocans*, USNM 1102483, Holocene, South Atlantic Ocean, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).
- Libystes** A. MILNE-EDWARDS, 1867, p. 285 [**L. nitidus*; M (ICZN Opinion 85, 1925, p. 15)] [= *Carcinoplacoides* KESLING, 1958, p. 235, pl. 3, 1–4, pl. 5, 8, pl. 7, 4–5, pl. 12, 19–23 (type, *C. flottei*, OD)]. Carapace transversely elliptical or quadrilateral, much wider than long, transversely flattened; front with two truncate lobes; upper-orbital margin entire; anterolateral margin entire or toothed; dorsal surface convex, smooth, with poorly defined regions; chelipeds subequal; pereopod 5 without paddle-like dactyli. *Pleistocene–Holocene. Pleistocene*: Japan, Guam. *Holocene*: Australia, Indo-West Pacific Ocean, Red Sea.—FIG. 11, 2a–b. *L. nitidus*, USNM 519523, Pleistocene, Guam, dorsal (a) and ventral (b) surfaces, scale bars, 1 cm (Schweitzer, Scott-Smith, & Ng, 2002, fig. 9.5–9.6).
- Neptocarcinus** LÖRENTHEY, 1898, p. 60 [**N. millenaris*; p. 60, pl. 4, 3–4; M]. Carapace wider than long, length about 60 percent carapace width; front wide, about 38 percent maximum carapace width; anterolateral margins with four lobes, last smallest; carapace regions not well marked. *Eocene (Ypresian–Priabonian). Eocene (Ypresian)*: Italy. *Eocene (Lutetian–Priabonian)*: Hungary, Italy.—FIG. 11, 3. **N. millenaris*, KSU D 1539, Lutetian–Priabonian, Hungary, scale bar, 1 cm (new).
- Rakosia** MÜLLER, 1984, p. 82 [**R. carupoides*; p. 82, pl. 68, 1–7; OD]. Carapace wider than long, transversely ovate, length about 65 percent maximum carapace width; front with two broad lobes and small inner-orbital lobes, front about 38 percent maximum carapace width; orbits wide, with at least one fissure; fronto-orbital width about 70 percent maximum carapace width; anterolateral margins with eight spines including outer-orbital spines, some appear to be paired, last anterolateral spine extending onto carapace as epibranchial ridge; carapace regions poorly defined. *Miocene (Langhian)*: Hungary, Poland.—FIG. 11, 4. **R. carupoides*, KSU D 1637, Miocene, Austria, scale bar, 1 cm (new).

Subfamily NECRONECTINAE Glaessner, 1928

[*nom. transl.* KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 105 ex Necronectidae GLAESSNER, 1928, p. 163] [=Gatuniidae RATHBUN, 1918, p. 168]

Carapace ovate; front with six spines; fronto-orbital width about 40–50 percent maximum carapace width; anterolateral margins with eight or nine spines including outer-orbital spine; regions poorly marked, carapace in general unornamented and relatively smooth, posterolateral and posterior margins rimmed; very small portion of sternite 8 visible in ventral view, sternum in general narrow for family, sternite 4 with axial groove extending anteriorly from sterno-pleonal cavity; male pleon triangular overall, weak remnants of sutures between somites 3/4 and 4/5, transverse keels on somites 2 and 3 generally with well developed transverse keels, somites 4 and 5 with well or poorly developed transverse keels or swellings; basal antennal article with laterodistal spines; chelae stout, may lack keels; fingers with molariform teeth along occlusal surface; meri of fifth pereopods much shorter than propodi; dactyls and propodi of fifth pereopods ovate to obovate in shape. [KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 105.] *Eocene–Holocene*.

Necronectes A. MILNE-EDWARDS, 1881, p. 1 [**N. vidalianus*; p. 1, pl. 21, 1; M] [= *Gatunia* RATHBUN, 1918, p. 168, (type, *G. proavita*, p. 168, pl. 54–56, pl. 58, 16–17, OD)]. Carapace wider than long; frontal margin with six small, blunt spines including inner-orbital spines; anterolateral margin longer than posterolateral margin, with eight triangular spines including outer-orbital spine, spine increasing in size posteriorly except last spine which is small; posterolateral margin concave; posterior margin rimmed; axial regions well developed. *Eocene–Pliocene. Eocene (Priabonian)*: France. *Eocene*: Spain. *Oligocene*: Antigua, Mexico (Baja

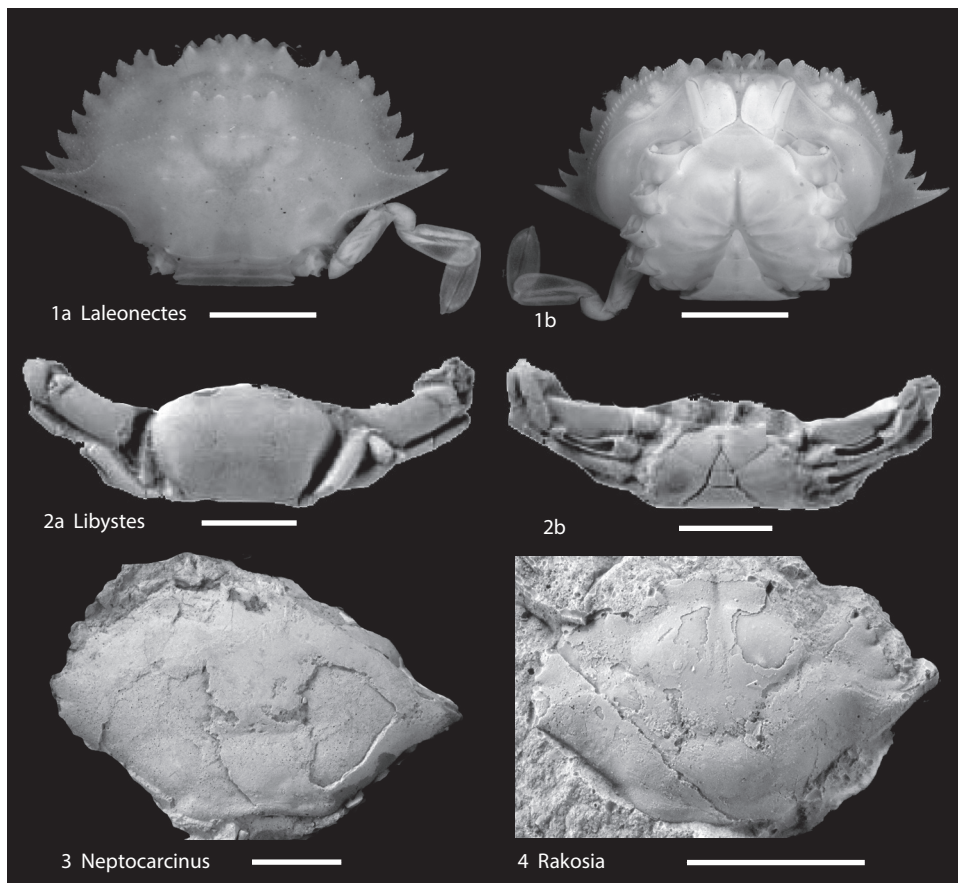


FIG 11. Portunidae (p. 22).

California Sur), Puerto Rico, USA (Florida, Mississippi). *Miocene (Burdigalian)*: Austria, Italy. *Miocene (Langhian)*: Hungary, Poland. *Miocene (Tortonian)*: Austria, Italy. *Miocene*: Ecuador, Mexico (Veracruz), Panama, Puerto Rico, Spain, Trinidad, USA (Maryland), Venezuela. *Pliocene*: Colombia.—FIG. 12, 1a–b. *N. collinsi* SCHWEITZER & others, 2006, USNM 527050, Miocene, Puerto Rico, dorsal (a) and ventral (b) views, scale bars, 1 cm (Schweitzer & others, 2006, fig. 5A,C).

Scylla DE HAAN, 1833 in 1833–1850, p. 11 [**Cancer serratus* FORSKÅL, 1775, p. 90; SD (RATHBUN in ICZN Opinion 73, Direction 37, 1922, p. 28)]. Carapace wider than long, ovate, regions poorly defined; front with six spines including inner-orbital spines, about half maximum carapace width; orbits directed forward, with two fissures; anterolateral margins with nine spines including outer-orbital spines, last spine longest; chelipeds strongly heterochelous, carpus with one to three spines on lower margin, mani massive, sometimes with weak keels on outer surface. *Eocene–Holocene. Eocene (Priabonian)*:

Java. *Eocene*: India, Pakistan. *Oligocene*: Germany. *Miocene (Langhian)*: Japan. *Miocene*: Austria, Brazil, Dominican Republic, France, Haiti, India, Japan, Pakistan, Puerto Rico, Switzerland. *Pliocene*: Guam, USA (Florida). *Pliocene*: Japan. *Pleistocene*: Guam, Japan, New Guinea. *Holocene*: Australia, Indo-Pacific Ocean, east Africa.—FIG. 12, 2a–b. **S. serrata* (FORSKÅL), USNM Silliman Univ. Ir6-86, Holocene, Philippines, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Subfamily LUPOCYCLINAE Paul'son, 1875

[Lupocyclinae PAUL'SON, 1875, p. 69]

Carapace ovate, somewhat wider than long, length about 80 percent maximum width; carapace ornamented with ridges and sometimes with large, spherical swellings; front protruding anteriorly, with four to

six spines or lobes including inner orbital; orbits directed forward, with two fissures, fronto-orbital width about 70–75 percent maximum carapace width; anterolateral margins tightly arched to nearly parallel to axis, usually bearing nine spines that may alternate in size, including the outer-orbital spine; anterolateral margins longer than posterolateral margins; posterolateral reentrant large; large portion of sternite 8 visible, slightly overlapping the third somite of the pleon in males; male pleon with somites 3–5 fused, somites 2 and 3 with transverse keels; basal antennal article simple; chelipeds slender, elongate, but shorter than other pereiopods; second to fourth pereiopods slender, elongate; meri of fifth pereiopod about equal to propodi with posterodistal spine; fifth pereiopod with oblancoolate dactyl. [KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 106.] *Miocene–Holocene*.

Lupocyclus ADAMS & WHITE, 1849, p. 46 [**L. rotundatus*, p. 47, pl. 12,4; M (ICZN Opinion 73, 1922, p. 27)]. Carapace subcircular, slightly wider than long; front projected, with four spines; upper orbital margin with two fissures; anterolateral margin with five large spines and small spines in each intervening notch, some or all of small spines sometimes obscured; dorsal surface convex with granulated ridges and elevations; chelipeds subequal, slender, longer than pereiopods. *Miocene–Holocene*. *Miocene–Pliocene*: Japan. *Holocene*: Australia, Indo-West Pacific Ocean, east Africa.—FIG. 12,3a–b. *L. quinquedentatus* RATHBUN, 1906, USNM 29667, Holocene, Hawaii, dorsal (*a*) surface and ventral (*b*) surfaces, scale bars, 1 cm (new).

Subfamily PODOPHTHALMINAE

Dana, 1851

[*nom. transl.* PAUL'SON, 1875, p. 69 *ex* Podophthalmidae DANA, 1851, p. 130]

Carapace much broader than long, widest about one-quarter to one-half the distance posteriorly on carapace; front narrow to extremely narrow at base and broadening distally to form a T-shape; orbits extremely broad, occupying about 80 percent to nearly entire anterior margin of carapace, entire or with fissures or notches; eyestalks very long, sometimes wider than carapace; anterolateral margin with two to nine spines

including outer-orbital spine; carapace often with transverse ridges on protogastric and branchial regions; epistomial spine well developed, visible dorsally; “antennules not completely retractile in fossae beneath front” (DAVIE, 2002, p. 456); basal article of antennae short and flagellum slender and long; sternum very broad, very broad portion of sternite 8 visible in ventral view, sternal suture 7/8 terminating well before sternopleonal cavity, sternal sutures 4/5, 5/6, 6/7, and 7/8 discontinuous; chelipeds very long, merus, carpus, and manus with spines, manus sometimes with keels; fifth pereiopod with paddle-like dactylus and postero-distal spines of meri. [KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 107.] *Eocene (Lutetian)–Holocene*.

Euphyllax STIMPSON, 1862, p. 225 [**E. dovii*, p. 226, pl. 5,5; M]. Carapace hexagonal, wider than long, length about 65 percent maximum width; front T-shaped, often with a sharp central spine; fronto-orbital width about 80 percent maximum carapace width; orbits with granular rim, sometimes with two closed fissures, sometimes with concave reentrant near outer-orbital spine; anterolateral margin short, with three to five spines, transverse ridge extending onto carapace from last anterolateral spine; protogastric and hepatic regions often with transverse ridges. [Emended from SCHWEITZER & others, 2006.] *Miocene–Holocene*. *Miocene*: Brazil, Costa Rica, Cuba, Haiti, Panama. *Pliocene*: Colombia, Panama. *Pleistocene*: Costa Rica, Jamaica. *Holocene*: Caribbean Sea, Pacific coastal Central America, Mexico, South America.—FIG. 13,1a–b. *Euphyllax domingensis* (RATHBUN, 1919), Miocene, Cuba; *a*, MNHNCu-P844, dorsal carapace; *b*, MNHNCu-P1822, ventral surface; scale bars, 1 cm (Schweitzer & others, 2006, fig. 6A, C).

Paraeuphyllax VARELA & SCHWEITZER, 2011, p. 14 [**P. cubaensis*, p. 14, fig. 1–3; OD]. Carapace wider than long, ovate, position of maximum width about half the distance posteriorly; orbits shallow, with two open fissures, fronto-orbital width about 70 percent maximum carapace width; front narrow, T-shaped, terminating in two reduced spines; anterolateral margin long for subfamily, with eight anterolateral spines excluding outer-orbital spines. [Emended from VARELA & SCHWEITZER, 2011, p. 14.] *Oligocene–Miocene*. *Late Oligocene–early Miocene*: Cuba. *Miocene*: Colombia.—FIG. 13,2a–b. **P. cubaensis*, late Oligocene–early Miocene, Cuba; *a*, holotype MNHNCu-93.002395, dorsal carapace; *b*, paratype MNHNCu-93.002396, ventral surface; scale bars, 1 cm (Varela & Schweitzer, 2011, fig. 1B, 2B).

Pheophthalmus FELDMANN, SCHWEITZER, & ENCINAS, 2010, p. 352 [**P. mochaensis*, p. 352, fig. 11; OD].

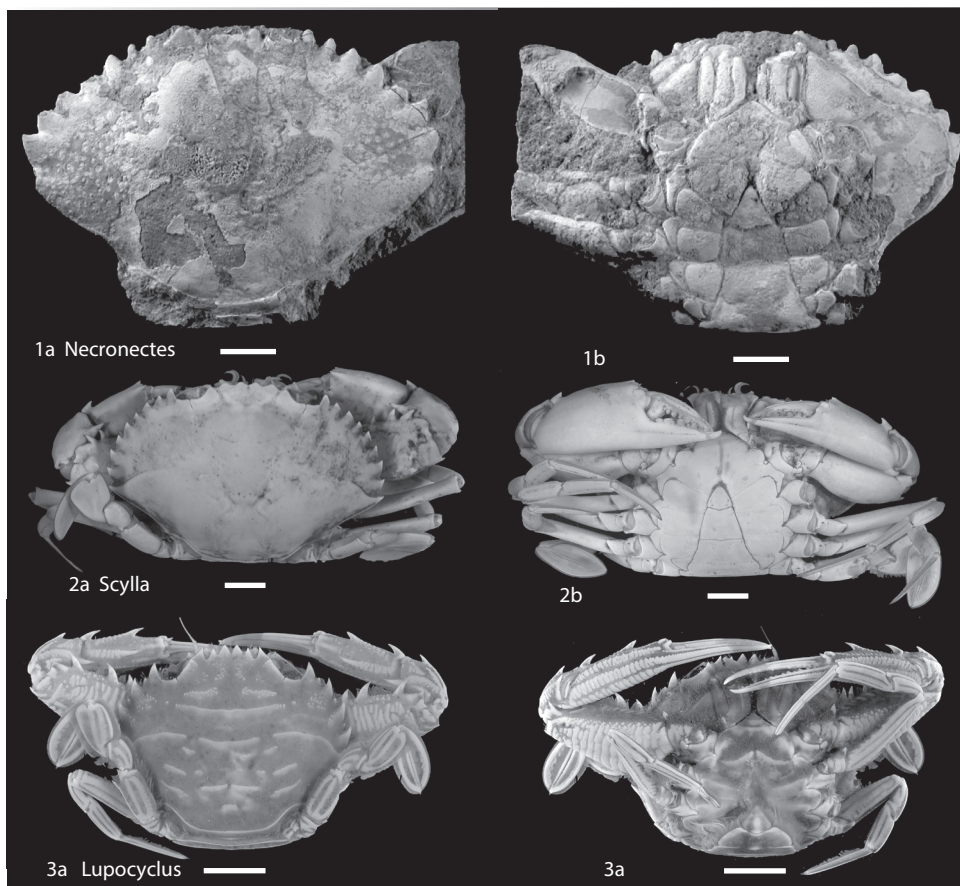


FIG 12. Portunidae (p. 22–24).

Carapace wider than long, widest at position of outer-orbital spines; upper-orbital margin serrate proximally, bearing nine spines distally including outer-orbital spine; lateral margins converging posteriorly, with one spine anteriorly, which extends onto carapace as epibranchial ridge, positioned very far anteriorly, remainder of branchial regions very long. [Emended from FELDMANN, SCHWEITZER, & ENCINAS, 2010, p. 352.] *Miocene*: Chile (Mocha Island).—FIG. 13,3. **P. mochaensis*, holotype SGO.PI 6595, Miocene, Chile, scale bar, 1 cm (FELDMANN, SCHWEITZER, & ENCINAS, 2010, fig. 11).

Podophthalmus LAMARCK, 1801, p. 152 [**Podophthalmus spinosus*; M; =*Portunus vigil* FABRICIUS, 1798, p. 363; =*Portunus vigil* WEBER, 1795, p. 93, *nom. nud.* (spelling corrected to *Podophthalmus*, LAMARCK, 1818, p. 257)]. Carapace wide, widest at outer-orbital angle, orbits oriented somewhat obliquely posteriorly; front T-shaped; orbits occupying maximum carapace width; lateral margins converging posteriorly, with two to four spines anteriorly. *Miocene–Holocene*. *Miocene*: Brunei, Taiwan.

Pleistocene: Australia, Guam, Japan, Java, Philippines, Sarawak. *Holocene*: Australia, Indo-Pacific Ocean, east Africa.—FIG. 13,4a–b. **P. vigil*, USNM 25389, Holocene, Hawaii, USA, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Psygmophthalmus SCHWEITZER, ITURRALDE-VINENT, HETLER, & VELEZ-JUARBE, 2006, p. 127 [**P. lares*, p. 128, fig. 6D; OD]. Carapace hexagonal, length about 60 percent carapace width, widest slightly more than half the distance posteriorly; front T-shaped, anterior end crenulate; fronto-orbital width about 80 percent maximum carapace width; orbits with two notches; anterolateral margins with five spines including outer-orbital spine; epibranchial region developed into arcuate ridge. [Emended from SCHWEITZER & others, 2006, p. 128.] *Miocene*: Anguilla, Puerto Rico.—FIG. 14,1. **P. lares*, holotype USNM 527076, Miocene, Puerto Rico, scale bar, 1 cm (Schweitzer & others, 2006, fig. 6D).

Sandomingia RATHBUN, 1919, p. 179 [**S. yaquiensis*, p. 180, pl. 8,1–2; M]. Carapace wider than long,

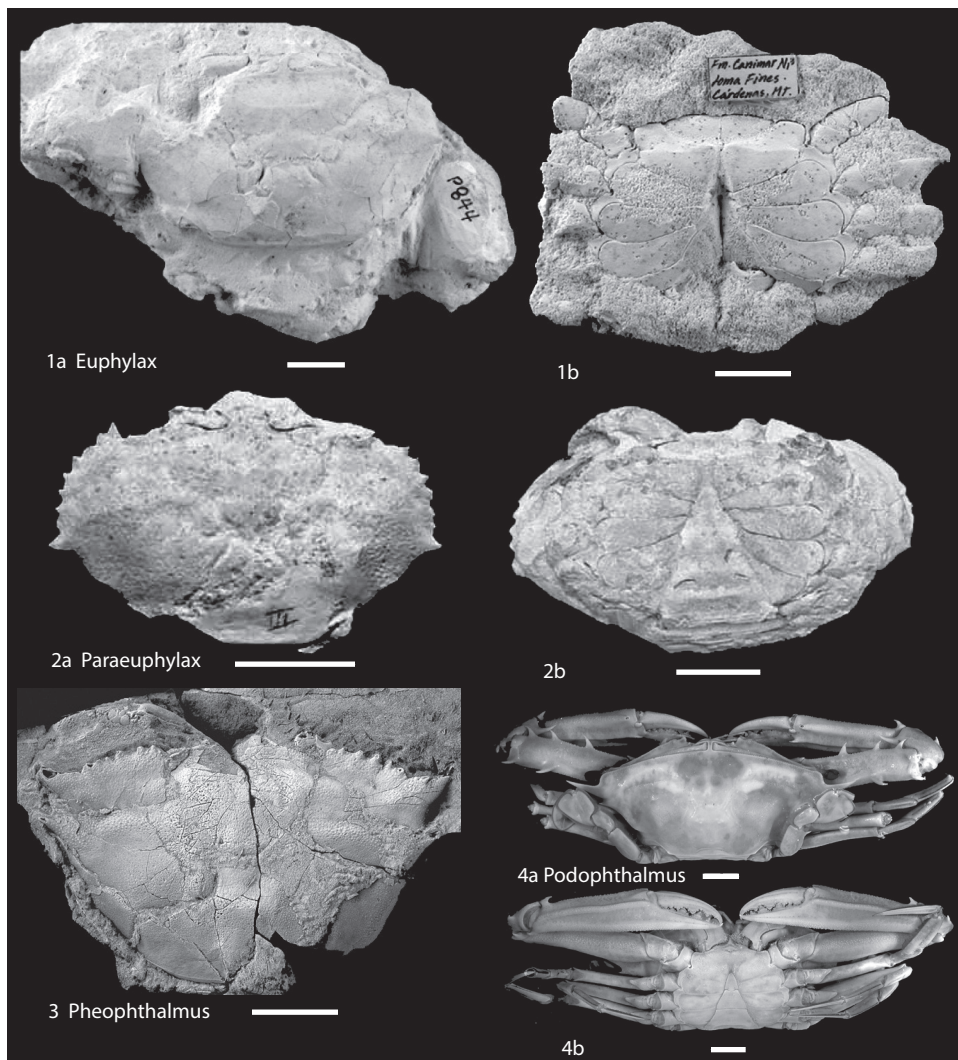


FIG 13. Portunidae (p. 24–25).

regions poorly defined; lateral margins converging posteriorly, with two spines anteriorly; postero-lateral reentrants large; posterior margin straight. *Miocene–Pliocene*: Costa Rica, Dominican Republic, Haiti.—FIG. 14, 2a–b. **S. yaquiensis*, USNM PAL 770870, Miocene, Dominican Republic, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Saratunus COLLINS, LEE, & NOAD, 2003, p. 213 [**S. longiorbis*, p. 213, pl. 5, 4; OD]. Carapace wider than long; front T-shaped, wide for family, orbits wide, rimmed, with two fissures, fronto-orbital width about 80 percent carapace width; anterolateral margins with six clearly differentiated spines; posterolateral margins concave; posterior margin straight; carapace regions moderately

defined. *Miocene*: Sabah, Sarawak.—FIG. 14, 3. **S. longiorbis*, holotype NHMUK IC 246, Miocene, Malaysia, scale bar, 1 cm (new).

Viaophthalmus KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 107 [**Ommatocarcinus zariquieyi* VIA, 1959, p. 59; OD]. Carapace not much wider than long; front triangular, orbits extremely elongate, extending beyond lateral margins of carapace into long, stout, outer-orbital spine; orbit with thickened rim, rim flared outward distally; lateral margins converging posteriorly; posterolateral reentrants moderately sized; protogastric regions with sharp, transverse keel extending continuously across both regions as well as mesogastric region, protogastric regions and anteriormost mesogastric

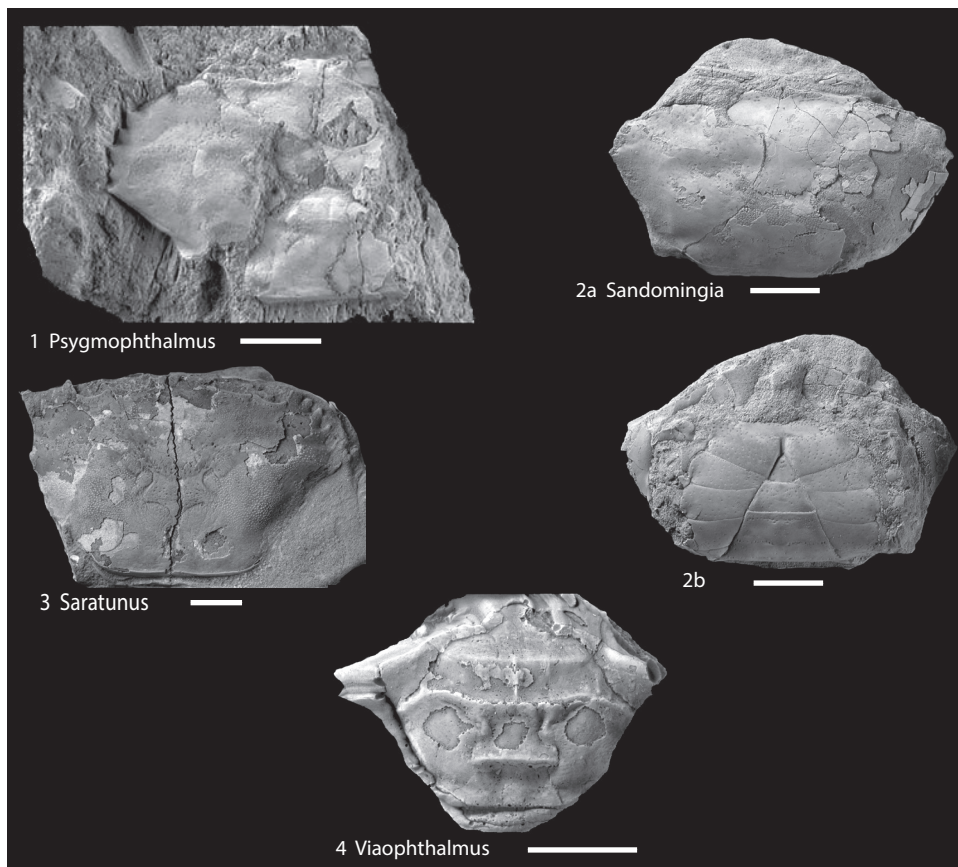


FIG 14. Portunidae (p. 25–27).

region united into ovate field; mesogastric region with longitudinal keel between protogastric and epibranchial keels; epibranchial keel arcing forward distally and then arcing posteriorly to become nearly straight as it crosses the axis; cardiac region with sharp transverse keel; male pleonal somites 3–5 fused, sutures weakly or not visible; sternum ovate, moderately wide, sternite 8 clearly visible in ventral view. [KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 107.] *Eocene (Lutetian)*: Spain.— FIG. 14, 4. **V. zariquieyi* (VIA), KSU D 193, cast of holotype MGSB 26404, scale bar, 1 cm (Karasawa, Schweitzer, & Feldmann, 2008, fig. 8).

Subfamily PORTUNINAE Rafinesque, 1815

[*nom. correct.* SAMOUELLE, 1819, p. 83 *pro* Portunidia RAFINESQUE, 1815, p. 97] [=Arenacinae DANA, 1851, p. 129; =Lupinae DANA, 1851, p. 129]

Carapace markedly wider than long, length ranging from about 55 to 75 percent

maximum carapace width, widest about 60 percent the distance posteriorly at position of last anterolateral spine, usually with arcuate epibranchial keel; front with six spines including inner orbital spines, front about one-quarter maximum carapace width but can range higher or lower (15–30 percent); orbits forward directed, fronto-orbital width about half maximum carapace width but can range higher or lower (35–60 percent); epistomial spine usually well developed, visible dorsally; basal article of antenna with laterodistal lobe or spine; antennal flagellum within the orbit; anterolateral margins generally with six to nine spines including outer-orbital spine, last spine usually notably longer or larger than other spines; male pleonal somites

3–5 fused, sometimes with weak remnants of sutures, somites 2 and 3 with transverse keels; lateral margins of male pleon can be markedly concave so as to be nearly T-shaped; large portion of sternite 8 visible in males, sternal sutures 4/5, 5/6, 6/7, and 7/8 discontinuous or with 6/7 complete; cheliped markedly longer than other pereopods, chelae generally with marked keels on outer surface; propodi and dactyli of fifth pereopod ovate; male first gonopod lacking subterminal spines. [Emended from KARASAWA, SCHWEITZER, & FELDMANN, 2008, p. 108.] *Eocene (Lutetian)–Holocene*.

Portunus WEBER, 1795, p. 93 [**Cancer pelagicus* LINNAEUS, 1758, p. 626; SD RATHBUN, 1926, p. 75 (ICZN Opinion 394, 1956, p. 317)]. Carapace much wider than long, regions moderately developed; frontal margin with six spines including inner-orbital spines; orbits with two closed fissures; anterolateral margin with nine spines including outer-orbital spines; chelae with well developed keels. [For complete synonymy of *Portunus* and its attendant subgenera, see NG, GUINOT, & DAVIE, 2008, p. 151–153; however, the genus *Portunus* is polyphyletic (KARASAWA, SCHWEITZER, & FELDMANN, 2008; MANTELATTO & others, 2009). Subsequent workers gave full genus status for some subgenera previously placed in the genus (i.e., NGUYEN & NG, 2010; SPIRIDONOV, NERETINA, & SCHEPETOV, 2014); therefore, the fossil species should be reevaluated]. *Paleogene–Holocene*. *Paleogene*: India, Italy. *Eocene (Lutetian)*: Hungary, Spain, Turkey. *Lutetian–Priabonian*: Hungary, Romania. *Priabonian*: India. *Eocene*: France. *Oligocene*: Croatia, Italy, UK (England). *Rupelian*: France, Italy, Puerto Rico. *Chattian*: Italy. *Oligocene–Miocene*: Cuba. *Miocene (Burdigalian)*: Croatia, France, Italy. *Burdigalian–Langhian*: Austria, Egypt, France, Hungary, Italy, Spain. *Langhian*: Hungary. *Langhian–Serravallian*: Italy. *Serravallian–Messinian*: Panama. *Serravallian–Tortonian*: USA (California). *Tortonian*: Austria, Hungary. *Miocene*: Austria, Brazil, Brunei, Indonesia (Celebes), Colombia, Croatia, Dominican Republic, Egypt, Fiji, France, Haiti, Hungary, Iran, Italy, Portugal, Romania, Mexico (Veracruz), Sabah, Sarawak, Spain, Taiwan, Trinidad, USA (Florida), Venezuela. *Pliocene*: Brunei, Costa Rica, Curaçao, Fiji, Italy, Japan, Sabah, Sarawak, Taiwan. *Pleistocene*: Australia (Queensland), Barbados, Jamaica, Panama, Taiwan, USA (California, Florida). *Holocene*: Cosmopolitan.—FIG. 15, 1. *Portunus anceps* (DE SAUSSURE, 1857), Holocene, Guadeloupe, French Territory, MNHN-IU-2013-6848 (photo by L. Corbari & S. Leprieur/MNHN).

Acanthoportunus SCHWEITZER & FELDMANN, 2002, p. 950 [**A. buchani*, p. 951, fig. 10; OD]. Carapace much wider than long; orbits wide, with two

fissures; anterolateral margin with eight spines including outer-orbital spine, last spine extremely long and is ornamented with two spines on upper surface; posterolateral margins sinuous; posterior margin rimmed; protogastric regions with two elongate tubercles; branchial regions with oblique row of tubercles; epibranchial region arcuate, extending from last anterolateral spine. *Eocene*: USA (California).—FIG. 15, 2. **A. buchani*, holotype, SDSNH 80155, scale bar, 1 cm (Schweitzer & Feldmann, 2002, fig. 10A).

Arenaeus DANA, 1851, p. 130 [**Portunus cribrarius* LAMARCK, 1818, p. 259; M (ICZN Opinion 73, 1922, p. 26); =*Lupa maculata* SAY, 1818 in 1817–1818, p. 445] [=*Eucenota* GERSTAECKER, 1856, p. 131 (type, *E. Mexicana*, M)]. Carapace wider than long, frontal margin with four spines including inner-orbital spines; orbits with intra-orbital spine bounded by open notches; anterolateral margin with nine spines, last spine longest; carapace regions poorly defined. *Miocene–Holocene*. *Miocene*: Cuba, Brazil. *Holocene*: Atlantic, Caribbean, northwestern South America.—FIG. 15, 3a–b. **A. cribrarius*, USNM 154779, Holocene, Georgia, USA, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Callinectes STIMPSON, 1862, p. 220 [**C. sapidus* RATHBUN, 1896, p. 352, pl. 12, 14–17; SD under ICZN Plenary powers, Opinion 712, 1964, p. 337; =*Portunus diacantha* LATREILLE, 1825, p. 190, suppressed by ICZN Opinion 712, 1964]. Carapace much wider than long, regions moderately developed; frontal margin with six spines including inner-orbital spines; orbits with two closed fissures; anterolateral margin with nine spines including outer-orbital spines; chelae with well-developed keels; male pleon distinctly T-shaped; telson of female very small compared to remainder of pleon. *Eocene–Holocene*. *Eocene (Lutetian)*: Jamaica. *Oligocene*: Panama; USA (Alabama). *Miocene (Aquitanian–Burdigalian)*: India. *Miocene*: Brazil, Costa Rica, Dominican Republic, India, USA (Florida, Virginia). *Pliocene*: Jamaica, Florida, USA (Virginia). *Pleistocene*: Jamaica, USA (California, Florida, Mississippi, New Jersey, North Carolina, South Carolina, Texas, Virginia). *Holocene*: Atlantic Ocean, Caribbean Sea, Mediterranean Sea, western Mexico.—FIG. 15, 4a–b. **C. sapidus*, USNM 1408398, Holocene, Atlantic Ocean, dorsal (a) and ventral (b) surfaces, scale bars, 1 cm (USNM collections [collections.nmnh.si.edu]).

Colneptunus LÖRRENTHEY in LÖRRENTHEY & BEURLEN, 1929, p. 180 [**Neptunus hungaricus* LÖRRENTHEY, 1898, p. 14, pl. 1, 1; SD GLAESSNER, 1969, p. 510] [=*Allogoneplax* VAN STRAELEN, 1934, p. 4 (type, *A. dallonii*, M); =*Gonioneptunites* VÍA, 1959, p. 47 (type, *N. hungaricus*, OD)]. Carapace wider than long, regions moderately defined; front with six spines including small inner-orbital spines; orbits with two fissures; anterolateral margins with eight spines, last one longest and penultimate spine smallest. *Eocene (Lutetian)*: Hungary, Senegal, Spain. *Eocene*: Hungary, Spain.—FIG. 15, 5. **C.*

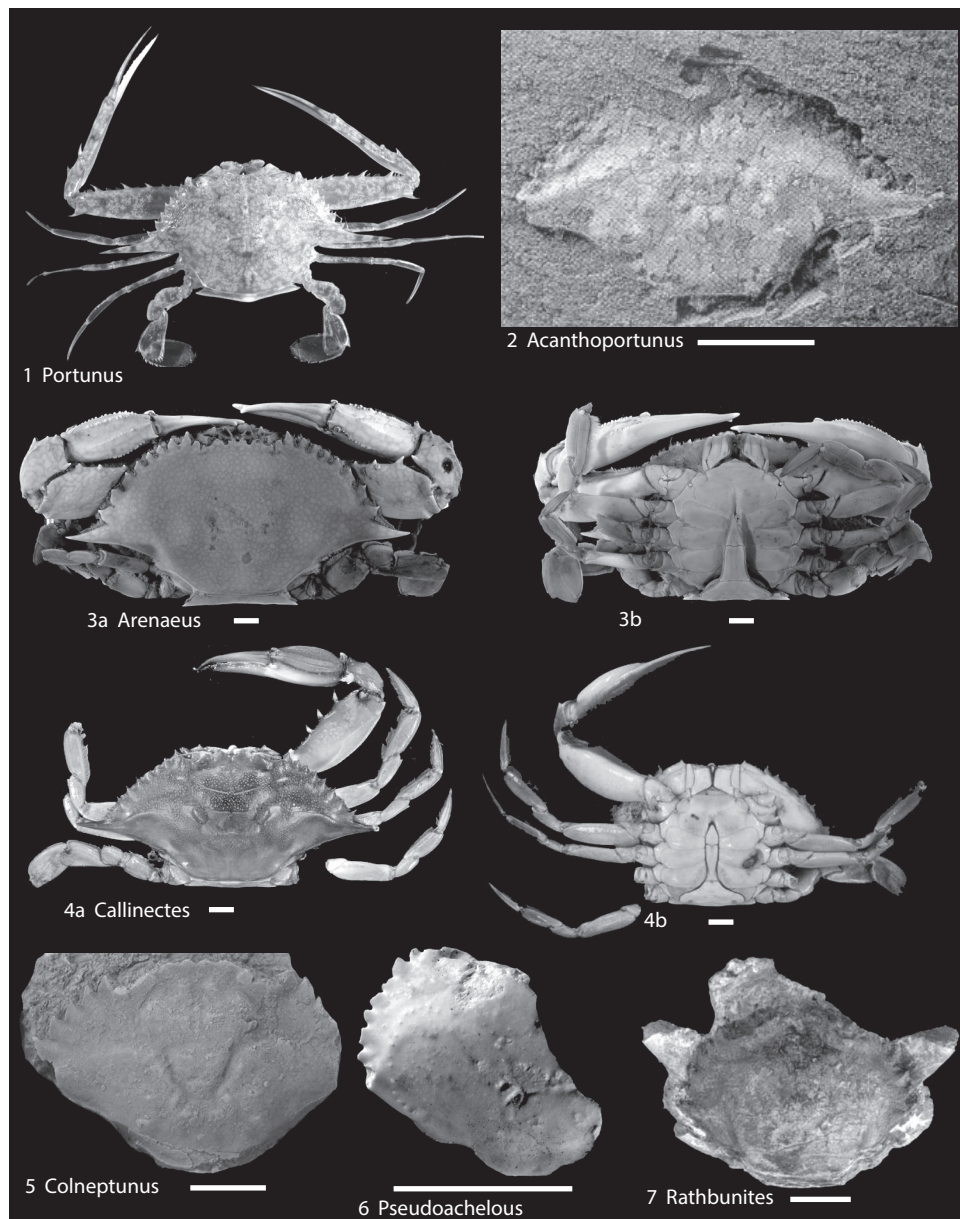


FIG 15. Portunidae (p. 28–30).

hungaricus, KSU D 214, cast of MGSB 16338, Lutetian, Spain, scale bar, 1 cm (new).

Pseudoachelous PORTELL & COLLINS, 2004, p. 118 [*P. schindleri*, p. 118, fig. 2, 1; OD]. Carapace wider than long; anterolateral margins with eight spines; carapace surface with tiny granules in arc subparallel to lateral margins. *Miocene*: Jamaica.—FIG. 15, 6. **P. schindleri*, holotype, UF 80478, scale bar,

1 cm (new; photo by R. Portell, Florida Museum of Natural History, Gainesville, Florida, USA).

Rathbunites SCHWEITZER, DWORSCHAK, & MARTIN, 2011, p. 362 [*Rathbunella pentaspinosa* COLLINS in COLLINS, PORTELL, & DONOVAN, 2009, p. 96, pl. 3, 5–6; OD] [= *Rathbunella*, p. 96, COLLINS in COLLINS, PORTELL, & DONOVAN, 2009 (type, *R. pentaspinosa*, OD), non *Rathbunella* JORDAN &

EVERMANN, 1896, p. 463 (Osteichthyes)]. Carapace wider than long, ovate, with five anterolateral spines excluding outer-orbital spine; orbits strongly oblique; regions poorly defined. *Miocene*: Dominican Republic.—FIG. 15,7. **R. pentaspinosa* (COLLINS), holotype NMB F 1417, scale bar, 1 cm (Collins, Portell, & Donovan, 2009, pl. 3,6).

Subfamily THALAMITINAE

Paul'son, 1875

[Thalamitinae PAUL'SON, 1875, p. 69] [=Caphyrinae PAUL'SON, 1875, p. 69; =Lissocarcinidae ORTMANN, 1893, p. 67]

Carapace wider than long; hexagonal to subcircular in shape; front with four to eight spines or lobes including inner-orbital; orbits generally broadly spaced, often positioned at the outer-most angles of the anterior margin of the carapace, orbits with two fissures, fronto-orbital width can range from about half maximum carapace width to nearly entire width; anterolateral margin with three to nine spines including outer-orbital spines, rarely entire, margin ranging from convex forward to nearly vertical to directed almost posterolaterally; posterolateral reentrant large; dorsal carapace often ornamented with transverse ridges on proto-gastric, hepatic, and epibranchial regions; basal article of antenna very wide, usually filling orbital hiatus, with laterodistal expansion; antennal peduncle and flagellum usually excluded from orbit; male sternum with crenate margins, lending an overall unique shape to the sternum among the Portunidae, shallow axial groove extending anteriorly from sterno-pleonal cavity onto sternite 4; male pleon with somites 3–5 fused, sometimes weak remnants of sutures visible, somite 2 with transverse keel, somites 1 and 3 sometimes with transverse keels; cheliped the same length or longer than other pereopods; fifth pereopods usually with paddle-like propodi and dactyli, carpus with small distal spine; merus with posterodistal spine; male gonopod 1 with subterminal spines. [Emended from KARASAWA, SCHWEITZER, & FELDMAN, 2008, p. 104, 109; EVANS, 2018, p. 40.] *Eocene* (*Ypresian*)–*Holocene*.

Thalamita LATREILLE, 1829, p. 33 [**Cancer admete* HERBST, 1803 in 1782–1804, p. 40, pl. 57,1;

M] [= *Thalamonyx* A. MILNE-EDWARDS, 1873, p. 168 (type, *Goniosoma danae* A. MILNE-EDWARDS, 1869, p. 153, pl. 7,6–7; SD (RATHBUN in ICZN, Opinion 73, Direction 37, 1922)]. Carapace wider than long; front with even number of lobes; orbits set at lateral ends of anterior margin of carapace, directed anterolaterally; anterolateral margins with five or six spines, often varying in size, alternating or with penultimate smallest; dorsal carapace with numerous, well-defined transverse ridges. *Miocene–Holocene*. *Miocene*: Taiwan. *Pliocene* (*Zanclean*): Italy. *Pliocene*: Japan, Taiwan. *Pleistocene*: China, Guam, Japan. *Holocene*: Australia, Indo-West Pacific Ocean, Red Sea.—FIG. 16,1. **T. admete* (HERBST), USNM 609445/UF 045494, *Holocene*, Hawaii, scale unknown (photo by G. Paulay, USNM collection [collections.nmnh.si.edu]).

Charybdis DE HAAN, 1833 in 1833–1850, p. 10 [**Cancer sexdentatus* HERBST, 1783 in 1782–1804, p. 153; SD GLAESSNER, 1929, p. 113; =*Cancer feriatus* LINNAEUS, 1758, p. 627; =*Cancer cruciatus* HERBST, 1794 in 1882–1804, p. 155] [= *Oceanus* DE HAAN, 1833 in 1833–1850, p. 9 (type, *Cancer crucifer* FABRICIUS, 1798, p. 364, M); = *Goniosoma* A. MILNE-EDWARDS, 1860, p. 263, unnecessary replacement name for *Charybdis*, ICZN Opinion 712, 1964] [For complete synonymy of *Charybdis* and its attendant subgenera, see NG, GUINOT, & DAVIE, 2008, p. 153–154]. Carapace wider than long, front with six or eight spines or lobes; fronto-orbital width about half to 65 percent maximum carapace width; anterolateral margins with six or seven spines including outer-orbital spine; carapace with more or less developed transverse ridges. *Eocene–Holocene*. *Eocene*: Italy. *Oligocene*: Italy. *Miocene* (*Langhian*): Hungary. *Miocene*: China, Hungary, Taiwan, Fiji. *Miocene–Pliocene*: Pakistan. *Pliocene*: Fiji, Japan, Taiwan. *Pleistocene*: Brunei, China, Sarawak, Taiwan, Japan. *Holocene*: Cosmopolitan.—FIG. 16,2a–b. *C. truncate* (FABRICIUS, 1798), USNM 55133, *Holocene*, Australia, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Cronius STIMPSON, 1862, p. 225 [**Portunus ruber* LAMARCK, 1818, p. 260; M; = *Goniosoma millerii* A. MILNE-EDWARDS, 1868, p. 54, pl. 18,1–3; = *Amphitrite edwardsii* LOCKINGTON, 1877, p. 43] [= *Charybdella* RATHBUN, 1897, p. 166 (type, *P. ruber*, M)]. Carapace wider than long; front wide, with six spines including inner-orbital spines; anterolateral margin with nine spines alternating in size; chelae very stout, with well-developed keels. *Pliocene–Holocene*. *Pliocene*: Fiji (claw only). *Holocene*: Atlantic Ocean, Caribbean Sea.—FIG. 16,3a–b. **C. ruber* (LAMARCK), USNM 59292, *Holocene*, Panama, dorsal (a) and ventral (b) views, scale bars, 1 cm (new).

Eocharybdis BESCHIN, BUSULINI, DE ANGELI, & TESSIER, 2002, p. 17 [**E. cristata*, p. 17, pl. 3,2; OD]. Carapace wider than long; front nearly straight, two broad lobes axially, small inner-orbital spines; orbits directed anterolaterally, with two fissures, fronto-orbital width about 65 percent maximum carapace width; anterolateral margins

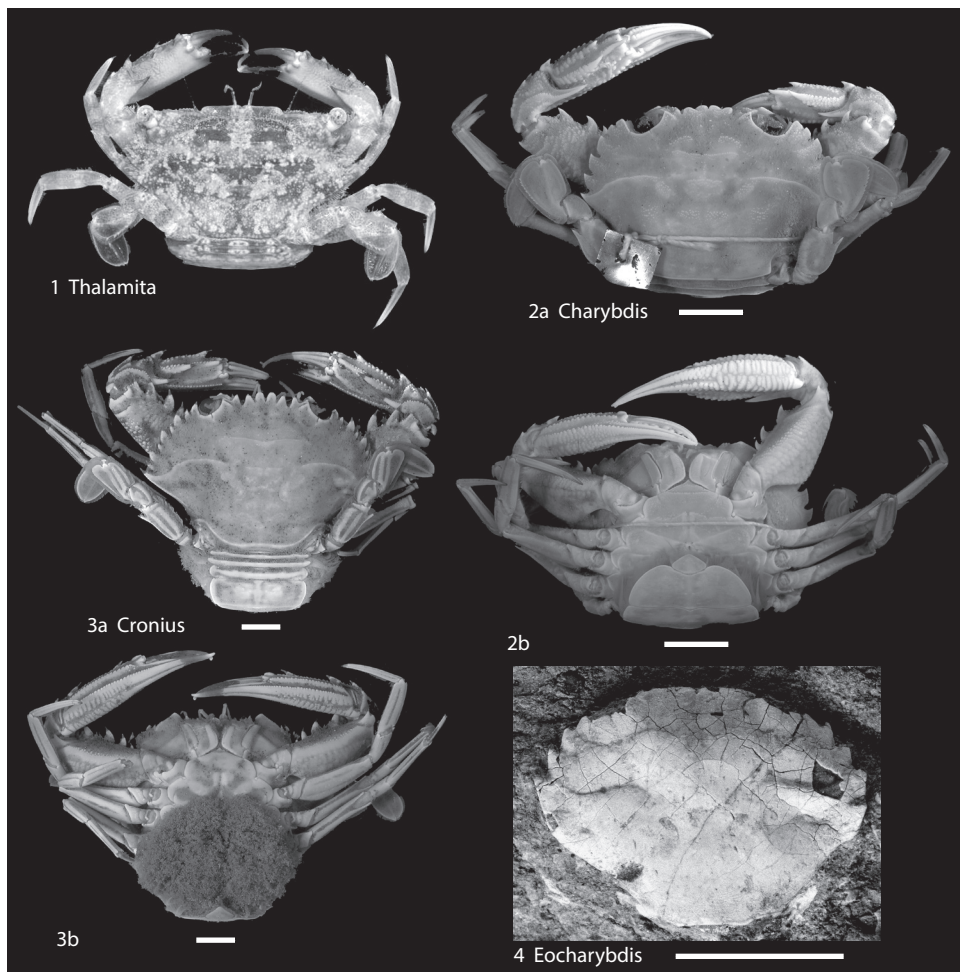


FIG 16. Portunidae (p. 30–31).

with four spines including outer orbital spines, weak ridge extending onto carapace between penultimate and last anterolateral spine; posterolateral margin concave; remainder of carapace smooth. *Eocene (Ypresian)*: Italy.—FIG 16,4. **E. cristata*, holotype MCZ I.G. 296403, scale bar, 1 cm (new; photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).

Lessinithalamita DE ANGELI & CECCON, 2015, p. 4 [**L. gioiae*, p. 5, fig. 3; OD]. Carapace wider than long; frontal margin very wide, more than half width of carapace; fronto-orbital width equal to maximum width of carapace; orbits directed anterolaterally, with two open fissures; anterolateral margins with four or five spines including outer-orbital spine; carapace regions moderately defined. *Eocene (Ypresian)*: Italy.—FIG. 17,1. **L. gioiae*, holotype MCZ I.G. 296403, scale bar,

1 cm (new; photo by A. De Angeli, Associazione Amici del Museo Zannato, Montecchio Maggiore, Vicenza, Italy).

Lissocarcinus ADAMS & WHITE, 1849, p. 45 [*L. polybioides*, p. 46, pl. 11,5; M] [= *Lissocarcinus* WHITE, 1847, p. 126, *nom. nud.*; = *Assecla* STREETS, 1877, p. 110 (type, *A. holothuricola*, SD NG, GUINOT & DAVIE, 2008, p. 148)]. Carapace about as wide as long or somewhat wider than long, hexagonal; front with two broad lobes axially and two small inner-orbital spines; orbits directed slightly anterolaterally; anterolateral margins with five lobes or small spines, last smallest; posterolateral margin concave, posterolateral reentrant large; posterior margin straight; chelipeds stout, pereiopods 2–4 short, pereiopod 5 with ovate manus and dactylus. *Miocene–Holocene. Miocene (Langhian)*: Hungary. *Holocene*: Indian Ocean, Indo-Pacific Ocean.—FIG. 17,2a–b. **L. polybioides*, USNM 1447134,

Holocene, Japan, dorsal (*a*) and ventral (*b*) views, scale bars, 1 cm (new).

- Mioxoiva** MÜLLER, 1978, p. 281 [**M. psammophila*, p. 281, pl. 16; OD]. Carapace about as wide as long, ovate; front with three small spines including inner-orbital spines; orbits forward directed, outer-orbital spine small, sharp; anterolateral margins with five small, sharp spines including outer-orbital spine. *Miocene (Langbian)*: Hungary.—FIG. 17,3. **M. psammophila*, holotype HNHM 86.266, scale bar, 5 mm (Müller, 1984, pl. 73,1; with permission of the Geological Survey of Hungary).
- Thalamitoides** A. MILNE-EDWARDS, 1869, p. 146 [**T. quadridens*, p.147, pl. 6,8–15; M (ICZN Opinion 73, 1922, p. 28); =*T. alphonsei* WARD, 1939, p. 3, fig. 3–4] [=*Hedrophthalmus* NAUCK, 1880, p. 67 (type, *H. thalamitoides*, M); =*Neothalamita* DEB, 1985, p. 173–175, pl. 1 (type, *N. triangularis*, OD)]. Carapace much wider than long; front very wide, with eight lobes; orbits placed at anterior corners, directed anterolaterally; lateral margins converging posteriorly, with four spines; dorsal carapace with transverse ridges. *Pliocene–Holocene. Pliocene–Pleistocene*: Marshall Islands. *Holocene*: Australia, Indo-West Pacific Ocean, Red Sea.—FIG. 17,4. **T. quadridens*, CBM-ZC 3773, Holocene, Japan; dorsal view, scale bar, 1 cm (photo by H. Kato, Natural History Museum and Institute, Chiba, Japan).

Family PSAMMOCARCINIDAE Beurlen, 1930

[*nom. transl.* KARASAWA, SCHWEITZER, & FELDMANN, 2008 p. 110
ex Psammocarcininae BEURLEN, 1930, p. 355]

Carapace frontal margin with three spines excluding inner-orbital spine, axial spine longest; orbits deep axially, shallowing laterally, inner-suborbital spine very long, visible in dorsal view; anterolateral margins with five spines including outer-orbital spine, last spine longest and with small spine on upper margin; small spine at posterolateral corner; axial and branchial regions well defined; dactyl of fifth pereopod oblancoolate. *Eocene (Bartonian)*.

- Psammocarcinus** A. MILNE-EDWARDS, 1860, p. 277 [**Portunus hericarti* DESMAREST, 1822, p. 87, pl. 5,5; M]. As for family. *Eocene (Bartonian)*: France.—FIG. 17,5. **P. hericarti* (DESMAREST), syntype MNHN F R03821, scale bar, 1 cm (new).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BSP: Bayerische Staatsammlung für Paläontologie und historische Geologie München (Munich), Germany
CBM: Natural History Museum and Institute, Chiba, Japan

- HNHM**: Hungarian Natural History Museum, Budapest, Hungary
IGM: Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, México City, México
KMNH: Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan
KSU D: Decapod Comparative Collection, Department of Geology, Kent State University, Kent, Ohio, USA
M: Hungarian Natural History Museum, Budapest, Hungary
MAB k: Oertijdmuseum, Boxtel, The Netherlands
MCZ-IG: Museo Civico “G. Zannato” di Montecchio Maggiore, Vicenza, Italy (I.G. = Inventario Generale dello Stato).
MFM: Mizunami Fossil Museum, Mizunami, Gifu, Japan
MGSB: Museo Geológico del Seminario de Barcelona, Barcelona, Spain
MGUH: Geologisk Museum, University of Copenhagen, Copenhagen, Denmark
MLP: Museo de la Plata, Division of Invertebrate Paleontology, La Plata, Argentina
MNHNCu-P: National Museum of Natural History, Paleontological collection, Havana, Cuba
MNHNF: Muséum National d’histoire naturelle, Paris, Collection de Paléontologie, Paris, France
MNHNIU: Muséum National d’histoire naturelle, Collection of Marine Invertebrates, Paris, France
NHMUK: Palaeontology Collections, The Natural History Museum, London, UK
NMB: Naturhistorisches Museum Basel, Switzerland
NZGS AR: New Zealand Geological Survey, Lower Hutt, New Zealand
PRI: Paleontological Research Institution, Ithaca, New York, USA
SDSNH: San Diego Museum of Natural History, San Diego, California, USA
SGO.PI: Museo Nacional de Historia Natural, Sección Paleontología, Santiago, Chile
USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
UF: Florida Museum, University of Florida, Gainesville, Florida, USA
UT: Jackson School Museum of Earth History, Non-Vertebrate Paleontology, University of Texas, Austin, Texas, USA
UWBM: Burke Museum, University of Washington, Seattle, Washington, USA

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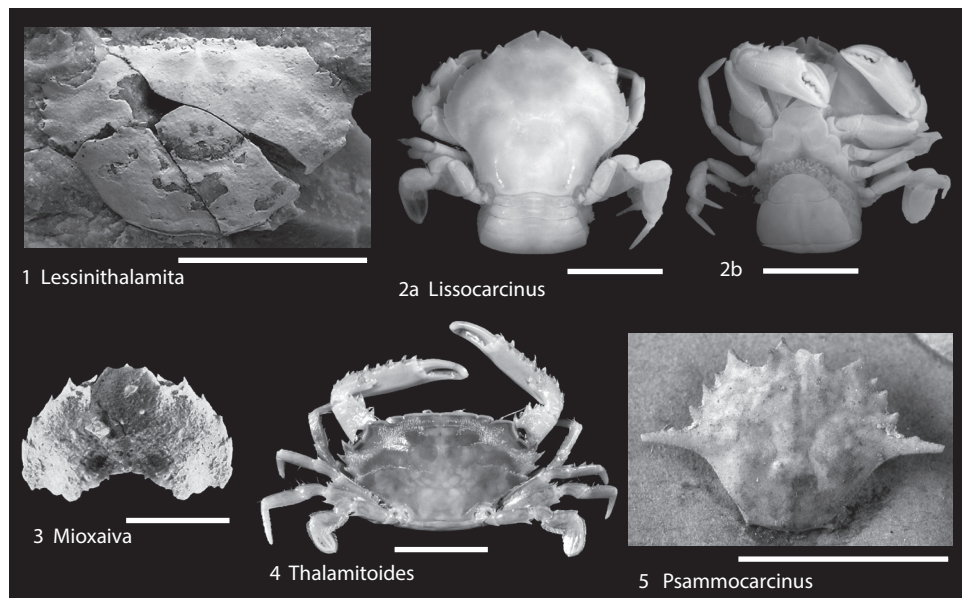


FIG 17. Portunidae, Psammocarinidae (p. 31–32).

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