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REVISION OF ETYIDAE GUINOT AND TAVARES, 2001 (CRUSTACEA: BRACHYURA)

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ABSTRACT—Members of the Etyidae and Feldmanniidae new family have unique arrangements of the spermatheca and gonopores that permit placement of each in different families and that differentiate each from all other brachyurans. Spermathecal openings are not always positioned along the sternal suture between sternites 7 and 8, suggesting that reproductive architecture within the Brachyura and what was formerly regarded as the Podotremata is considerably more diverse and disparate than previously thought. Etyidae and Feldmanniidae radiated in the early Cretaceous and survived into the Paleogene. New taxa include *Steorrosia* new genus, *Bretonia* new genus, *Faksecarcinus* new genus, and sixteen new combinations.

INTRODUCTION

IT HAS been known for some time that Cretaceous brachyurans are difficult to place within existing superfamily and family classifications and that new groups must be erected to accommodate them (Guinot and Tavares, 2001; Karasawa et al., 2008; Feldmann et al., 2007; Feldmann et al., 2008; Schweitzer and Feldmann, 2010). Among the brachyurans of the Cretaceous, there are several podotrematous forms that are wider than long and that have a generally dynomenid or even xanthoid appearance that have proven to be difficult to classify. Guinot and Tavares (2001) demonstrated the podotrematous nature of some members of this group, placing three genera, *Etyus* Leach in Mantell, 1822; *Feldmannia* Guinot and Tavares, 2001; and *Xanthosia* Bell, 1863 within the Etyidae Guinot and Tavares, 2001. However, Guinot and Tavares (2001) recognized the heterogeneous nature of the genus *Xanthosia* by placing some species within it and excluding other species, leaving them unplaced at the generic level. Later, De Grave et al. (2009) and Schweitzer et al. (2010) placed several genera within Etyidae. Schweitzer et al. (2010) also recognized the heterogeneity of *Xanthosia* by listing some species as being members of the genus (p. 67) and others as "*Xanthosia*" sensu lato (p. 131).

Examination of holotype, paratype, and topotype material of species of genera referred to Etyidae indicates that *Feldmannia* is not a member of Etyidae and should be removed to a new family along with other taxa. In addition, the history of placement of species into *Xanthosia* has been complicated, resulting in an ever-broadening definition of the genus. We examined holotype specimens, and other referred material, of nearly every species that has been historical referred to *Xanthosia* (Table 2). The result is a comprehensive revision of the genus, and as a result the Etyidae.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations.—BMNH, The Natural History Museum, London, U.K.; KSU D, Decapoda Comparative Collection, Department of Geology, Kent State University, Kent, Ohio, U.S.A.; MAB, Oertijdmuseum De Groenepoort, Boxtel, The Netherlands; MGSB, Museo Geológico del Seminario de Barcelona, Spain; MGUH, Geological Museum, Copenhagen, Denmark; MNHN, Museum National d'Histoire Naturelle, Paris, France; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NJSM, New Jersey State Museum, Trenton, New Jersey, U.S.A.; OUM, Geological Museum, Oxford University, Oxford, U.K.; SDSM, SDSMT, South Dakota School of Mines and Technology, Rapid City, South Dakota, U.S.A.; SM, Sedgwick Museum, Cambridge University, Cambridge, U.K.; UCMG, University of Colorado Museum of Natural History, Invertebrate Paleontology, Boulder, Colorado, U.S.A.; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Infraorder BRACHYURA Linnaeus, 1758
Section ETYIOIDA Karasawa et al., 2011
Superfamily ETYIOIDEA Guinot and Tavares, 2001
Family ETYIDAE Guinot and Tavares, 2001

Included genera.—*Etyus* Leach in Mantell, 1822; *Etyxanthosia* Fraaije et al., 2008; *Guinotosia* Beschin, Busulini, De Angeli, and Tessier, 2007; *Secretanella* Guinot and Tavares, 2001; *Sharnia* Collins and Saward, 2006; *Steorrosia* new genus; *Xanthosia* Bell, 1863.

Diagnosis.—Carapace wider than long, length ranging from half to two-thirds maximum carapace width (maximum carapace width measured between bases of spines, if present); position of maximum width 50–66% the distance posteriorly on carapace; anterolateral margins with four to seven spines, spines may be small or large, margin generally somewhat shorter than posterolateral margins; fronto-orbital width ranging from 35–60% maximum carapace width; posterolateral margin generally concave but may be sinuous; regions generally well defined, ornamented with granules or tubercles of varying sizes or nearly smooth; cervical groove initiating along anterolateral margin from 35–50% the distance posteriorly, crossing the midline at about half the distance posteriorly, beginning along anterolateral margin, arcing concave forward, then convex forward at base of protogastric region, then concave forward around base of mesogastric region about half the distance posteriorly. Epibranchial region composed of a distal area that embraces last anterolateral spines bounded anteriorly by cervical groove and usually posteriorly by an oblique groove extending posterolaterally from cervical groove and intersecting posterolateral margin (branchial groove 1: bg1); mesobranchial region almost always developed as a more or less oblique ovate region bounded anteriorly by cervical groove, laterally by bg1 (Fig. 1), and usually axially by another oblique groove extending posterolaterally from cervical groove and intersecting posterolateral margin (branchial groove 2: bg2) (Fig. 1), bg1 or bg2 always present, usually both; metabranchial region flattened.

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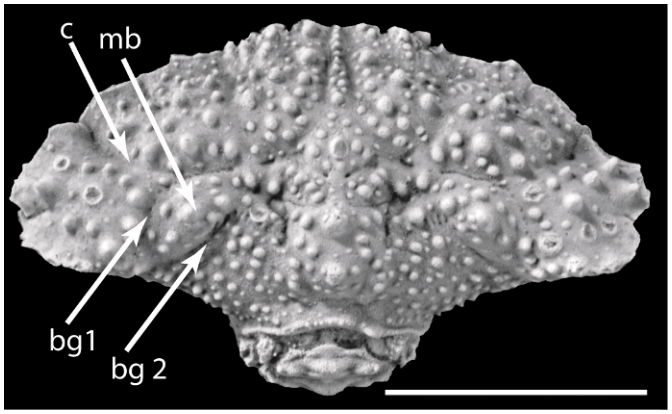

FIGURE 1—Dorsal carapace of *Steorrosia aspera* (Rathbun, 1935), a member of Etyidae, USNM 543680, showing the position of the cervical groove (c), mesobranchial region (mb), branchial groove 1 (bg1), and branchial groove 2 (bg2). Possession of some combination of these features is diagnostic for Etyidae. Scale bar=1 cm.

Female sternum narrow, deep; sternites 1–3 triangular, separated from sternite 4 by suture; sternite 4 with rectangular anterior process, pereiopod 1 articulating at intersection between anterior process and episternal projection which is directed laterally and upward at about 45° angle to flat sternal cavity; sternite 5 with large episternal projections directed laterally and upward at about 45° angle to flat sternal cavity, articulating with pereiopod 2; sternites 5 and 6 separated by complete suture; sternite 6 with episternal projections directed posterolaterally, articulating with pereiopod 3; sternites 7 and 8 directed strongly posterolaterally, wider than long, 8 longer than 7; external opening of spermatheca may be situated entirely on sternite 7 (Fig. 2.3, 2.4), apparently not as part of suture between 7 and 8, transversely ovate, surrounded with granules, anterior and axial edge of sternite 7 raised and rotated ventrally (*Steorrosia*); spermatheca may be situated along sternal suture 7/8 in some taxa (*Etyus*); anterior end of sternite 8 overlapping posterior end of sternite 7.

Pleon wide in both males and females; all pleonites free. Female pleonites wide, covering part of coxae of pereiopods; pleonites 1–6 with axial swellings; coxae 1–5 with lateral swellings; pleonites with depressed rim along posterior margin; pleonites 6 twice as long as other pleonites; telson locking into coxae of pereiopods 1, with longitudinal groove; posterior margin of pleonites sinuous, with posteriorly directed projection axially. Male pleon similar in form to female but narrower and flatter.

Third maxillipeds longer than wide; in two planes. Pereiopods decreasing in size posteriorly; coxae of pereiopod 1 with abdominal locking mechanism; coxae of pereiopod 3 with female gonopores, gonopores situated on ventral surface and close to sternal edge of coxa, position of gonopores just anterior to spermathecal opening (Fig. 2.3, 2.4); pereiopod 5 carried at least subdorsally and possibly fully dorsally, reduced in size compared to other pereiopods (for illustrations of anatomical terminology used herein, see McLaughlin, 1980, figs. 51, 52).

Discussion.—The Etyidae are most easily diagnosed and recognized dorsally by their wider than long carapace; spinose anterolateral margins; sinuous cervical groove that is initially concave forward, then arcs convex forward, then concave forward around the base of the mesogastric region; varyingly developed oblique mesobranchial region bounded by branchial grooves 1 and 2 (Fig. 1); and usually well-developed axial regions of the carapace. Not all have both bg1 and 2 but all have at least one of these grooves, and all have at least a weak swelling in the position of the mesobranchial region. Of those with known sterna and abdomina, the female abdomina are wide and inflated, and somite 6 is long. Unfortunately, only a few taxa are known with well-preserved sterna and abdomina, so assignment to the family is usually done based upon dorsal carapace morphology. The possession of coxal gonopores and sternal spermatheca places the Etyidae squarely within the less derived brachyurans.

Two genera were named in the nineteenth century to accommodate Cretaceous brachyurans that were markedly longer than wide and that had generally well-marked carapace regions, *Etyus* and *Xanthosia* Bell, 1863. Over time, *Xanthosia* became the catch-all genus for crabs with this shape, and *Etyus* remained a monotypic genus, perhaps because of its confluent protogastric and hepatic regions, granular ornamentation, and small anterolateral spines. Measurement of various aspects of the shape of the carapace, the position of the grooves and spines, the length of the various margins, and features other than the ornamentation and the overall shape of the carapace (ovate and wider than long) indicate that many of the species originally referred to *Xanthosia* are better placed within *Etyus* and that many must be referred to new genera altogether, described below.

Examination of dozens of well-preserved specimens of *Feldmannia* indicates that they differ markedly from members of Etyidae, and they are herein removed to a new family described below. Thus, membership in Etyidae is herein restricted.

Genus ETYUS Leach in Mantell, 1822

Type species.—*Etyus martini* Mantell, 1844, by subsequent monotypy.

Other species.—*Etyus buteonis* (Wright and Collins, 1972); *E. granulosa* (M'Coy, 1854b); *E. jacksoni* (Wright and Collins, 1972); *E. sakoi* (Karasawa et al., 2008); *E. similis* Bell, 1863.

Diagnosis.—Carapace transversely ovate, wider than long, widest about 60% the distance posteriorly on carapace; orbits circular, directed forward; fronto-orbital width usually half but may be about 35% maximum carapace width; anterolateral margins convex, with four or five spines, spines may be small and blunt, sharp, or large and rectangular; posterolateral margin concave, about same length or slightly longer than anterolateral margin. Axial regions moderately defined, mesogastric region triangular; protogastric and hepatic regions usually well-differentiated but may be confluent; branchial regions subdivided into three distinct areas; epibranchial region composed of a distal area that embraces last anterolateral spines bounded anteriorly by cervical groove and posteriorly by bg1; mesobranchial region developed as an oblique ovate region bounded anteriorly by cervical groove, laterally by bg1, and axially by bg2; metabranchial region flattened. Cervical groove beginning along anterolateral margin about half the distance posteriorly, arcing concave forward, then convex forward at base of protogastric region, then concave forward around base of mesogastric region about half the distance posteriorly; ornamentation usually tubercles but may be granular, granules may be all of one size or with interspersed larger tubercles.

Sternite 3 and sometimes 4 visible even with pleon in place; spermathecal openings long, ovate, situated posteriorly; all abdominal pleonites free in males and females, telson long, triangular (Fig. 3.7).

Material examined.—*Xanthosia buteonis*, holotype, (BMNH) In.60958; *Xanthosia granulosa*, (BMNH) In.29736, 29737,

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29920–1; SM B22656; *Xanthosia jacksoni*, (BMNH) In.60957, holotype; *Etyus similis*, SM B22637; *Etyus martini*, KSU D 1751, D 1516, cast of J.S.H. Collins collection 2367j.

Discussion.—Several species originally referred to *Xanthosia* by Wright and Collins (1972) display a range of characters and preservational styles. When their morphological characters are compared to those of the type species of both *Etyus* and *Xanthosia*, it is clear that they have an affinity with the type species of *Etyus*, *Etyus martini*, and not that of *Xanthosia*. Note that *Xanthosia similis* was originally referred to *Etyus* by Bell (1863) and was later referred to *Xanthosia* by Carter (1898). By examining the range of variation among the various characters displayed by *Etyus martini*, *X. similis*, *X. granulosa* and *X. buteonis*, clear patterns do not emerge (Fig. 3). For example, the spines are variable among these species, but the morphology of the spines does not correspond to specific patterns of ornamentation of the carapace. The fronto-orbital width is about half the carapace width in all except *E. martini*, in which it is about 35%. All have the position of maximum width positioned about two-thirds the distance posteriorly except *X. similis*. All have moderately deep grooves and tubercles except *X. granulosa*, which has shallow grooves and is granular. *Xanthosia sakoi* has long protogastric and hepatic regions and long anterolateral margins with a maximum width positioned over half the distance posteriorly. Thus, this would suggest that either all could be placed within *Etyus*, or each would require a separate genus to accommodate their one or two unique characteristics.

We suggest that all be placed within *Etyus* for the following reasons. First, it seems unnecessary to erect a new genus for each of five species based on one or two differences when all other features fit the generic concept presented herein. Of these taxa, both *E. martini* and *X. granulosa* possess abdomina that are similar to one another. They are also the two species that are end members in terms of dorsal carapace ornamentation; thus, they are different from one another somewhat dorsally, but their pleons are similar. Granted, if they belong to the same family, this would be expected. Another reason to place all five of these species within *Etyus* is the poor preservation of some of the species. The holotype of *Xanthosia buteonis* is poorly preserved and lacks cuticle, and the paratype is a fragment (Fig. 3.4). Internal molds and specimens without cuticle can be misleading, because they present different information on ornamentation, groove depth, and other surface features than do specimens with preserved cuticle (Schweitzer et al., 2009). Thus, it is possible that some of the species named based upon internal molds or decorticated material could be synonymous with species named based upon specimens with cuticle. In addition, examination of figs. 2a and 4a on plate 20 in Wright and Collins (1972), which were referred to *X. granulosa* and *X. fossa* respectively, are both internal molds but referred to two different species even though they look similar to one another. Thus, it would be imprudent to base new genera on this incomplete material, and we suggest referral of all five of these species to *Etyus* until new collections can be made that might help to clarify the various morphological characters within and among these species.

Xanthosia jacksoni is problematic. The specimen is tiny (6 mm wide) and poorly preserved; the front is broken as is the left anterolateral margin (Fig. 3.3). Black paint has been applied around the margins of the carapace which may obscure the true size of the anterolateral spines and the shape of the carapace. Most of the dorsal carapace cuticle is missing. Examination of the carapace features that are preserved suggests that *Xanthosia jacksoni* is most similar to *Etyus granulosa* (Fig. 3.6, 3.8, 3.9), based upon its lack of well-developed regions, its granular ornamentation, crispate anterolateral margins with small triangular spines (four excluding the outer orbital margins); wide, concave posterior margin; length to the origin of the cervical groove along the anterolateral margin (about 45% the distance posteriorly); and possession of a weak bg1. The existence of only one poorly preserved specimen makes this placement rather provisional, but for now, we place the species in *Etyus*, resulting in *Etyus jacksoni* new combination.

The oldest species is *Etyus sakoi* from the Barremian of Japan. The remaining species are known from the late Early Cretaceous of Britain, suggesting a possible northerly dispersal route.

GENUS XANTHOSIA Bell, 1863

For complete synonymy, see GUINOT AND TAVARES (2001, p. 516).

Type species.—*Xanthosia gibbosa* Bell, 1863, by subsequent designation of Glaessner (1929, p. 401; reiterated by Glaessner, 1969, p. R488). Glaessner (1929) was the first to refer *Podophthalmus buchii* to *Xanthosia*, but he did not synonymize it with *X. gibbosa*; Wright and Collins (1972, p. 98) synonymized *Xanthosia gibbosa* and *X. buchii*. Examination of the syntypes of *X. gibbosa* and the holotype of *X. buchii* indicates that these two species are not synonymous. *Xanthosia buchii* was originally referred to *Podophthalmus* by Reuss (1845). Glaessner (1929, p. 401) designated *X. gibbosa* as the type species of *Xanthosia*, as it will remain.

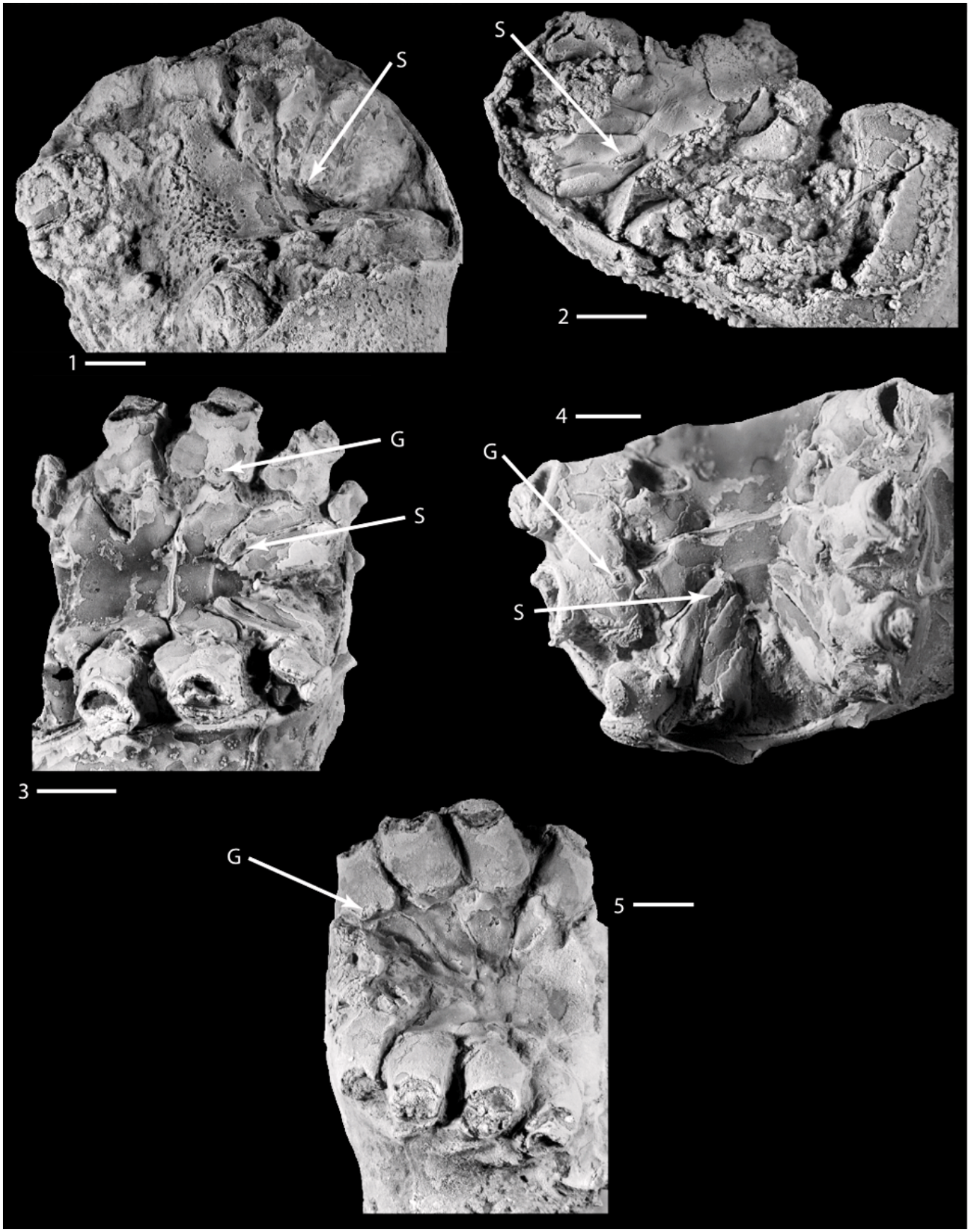
Included species.—*Xanthosia elegans* Roberts, 1962; *X. fischeri* (A. Milne-Edwards, 1862); *X. gibbosa*; *X. semiornata* Jagt, Collins, and Fraaye, 1991, questionably.

Diagnosis.—Carapace transversely ovate, wider than long, length about 58% maximum carapace width, position of maximum width about 60% the distance posteriorly on carapace; front poorly known, axially sulcate; orbits directed forward, fronto-orbital width about 55% maximum carapace width; anterolateral margins nearly straight or slightly convex, with at least five sharp spines; anterolateral margins shorter than posterolateral margins; posterolateral margins sinuous, initially convex, then concave; posterolateral margins broadly concave. Axial regions moderately defined, mesogastric region triangular; protogastric and hepatic regions well-differentiated; branchial regions subdivided into three distinct areas; epibranchial region composed of a distal area that embraces last anterolateral spines bounded anteriorly by cervical groove and posteriorly by bg1; epibranchial region developed as a more or less oblique ovate region bounded anteriorly by cervical groove, laterally by bg1, and axially by bg2; metabranchial region flattened. Cervical groove beginning along anterolateral margin about 40% the distance posteriorly, arcing concave forward, then convex forward at base of protogastric region, then concave forward around base of mesogastric region about 55% the distance posteriorly. Carapace ornamentation ranging from granular to small tubercles, rarely, as large, spherical swellings.

Pereiopod 5 carried subdorsally; female? abdominal pleonites wide, at least one through four free.

Material examined.—*Xanthosia gibbosa*, syntypes (BMNH) In.29964, 29966, 36647, 59523; *Podophthalmus buchii* Reuss, 1845, holotype, NHMW 1864.XL.604; *Xanthosia elegans*, NJSM GP22689. We did not find a specimen of *Xanthosia fischeri* (Fig. 4.2) in the MNHN in 2010.

Discussion.—Several attempts have been made to revise the genus *Xanthosia*, which has been recognized for some time as being unwieldy. Schweitzer Hopkins et al. (1999) suggested that there may be several morphotypes within the genus such that it may require splitting. Guinot and Tavares (2001) restricted the



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membership within *Xanthosia* without referring the excluded species to other genera. Fraaije et al. (2008) made a further attempt to restrict membership in *Xanthosia* with the addition of another genus, *Etyxanthosia*. By documenting a wide variety of morphological features, we have determined that only four species should be referable to *Xanthosia* sensu stricto by comparison of features with the type specimens of the type species wherever possible.

Herein, we define *Xanthosia* in the strict sense as having the features within the diagnosis above. Key among these are a cervical groove that begins rather close to the anterior edge along the anterolateral margin, about 40% the distance posteriorly; a relative short anterolateral margin; a sinuous posterolateral margin; and sharp spines. These features differentiate it from its most similar genus, morphologically, *Etyus*.

XANTHOSIA GIBBOSA Bell, 1863
Figure 4.1

Xanthosia gibbosa BELL, 1863, p. 3, pl. 1, figs. 4–6. GLAESSNER, 1929, p. 402; GLAESSNER, 1969, p. R488; SCHWEITZER et al., 2010, p. 67.

Xanthosia buchii (REUSS, 1845) sensu WRIGHT AND COLLINS, 1972, pl. 20, figs. 3a–c.

Non Podophthalmus buchii REUSS, 1845, p. 15, pl. 5, fig. 50.

Diagnosis.—Carapace widest about 60% the distance posteriorly; fronto-orbital width about 60% maximum carapace width; anterolateral margin shorter than posterolateral margin, weakly convex, with five sharp triangular spines including outer-orbital; posterolateral margin sinuous; cervical groove initiating along anterolateral margin about 40% the distance posteriorly on carapace; oblique mesogastric region weak.

Description.—Carapace transversely ovate, wider than long, widest at position of last anterolateral spine about 60% the distance posteriorly. Front axially sulcate, otherwise shape unknown, frontal width about 45% maximum carapace width; orbits appearing to have been shallow, directed weakly anterolaterally, slightly deeper axially than laterally, rimmed, weak outer-orbital spine, fronto-orbital width about 60% maximum carapace width. Anterolateral margin shorter than posterolateral margin, weakly convex, about 70% length of posterolateral margin, appearing to have had five triangular, sharp spines including outer-orbital spine. Posterolateral margin convex anteriorly, then concave; posterior margin concave, about 38% maximum carapace width.

Mesogastric region triangular, with elongate swelling anteriorly on narrow anterior extension, length to base of mesogastric region about 55% maximum carapace width; protogastric regions trapezoidal bounded by deep grooves, with granular ornamentation; hepatic region wider than long, granular; cervical groove extending from lateral margin between third and fourth anterolateral spines in concave forward path, then arcing slightly convex forward at base of protogastric region, then concave forward around base of mesogastric region, cervical groove initiating along anterolateral margin about 40% distance posteriorly on carapace. Branchiocardiac groove appearing to be developed only as arcuate depressions alongside metagastric, urogastric and cardiac regions. Metagastric and urogastric regions united into long, inflated region which itself merges with cardiac region. Branchial regions subdivided into three distinct areas; epibranchial region composed of a distal area that embraces anterolateral spines 4 and 5, bounded anteriorly by cervical groove and posteriorly by bg1; mesobranchial region developed as a more or less oblique ovate region bounded anteriorly by cervical groove, laterally by bg1, and axially by bg2; metabranchial region flattened.

Ventral surface and appendages unknown.

Types.—*Xanthosia gibbosa*, syntypes (BMNH) In.29964, 29966, 36647, 59523.

Occurrence.—Upper Greensand (lower Cenomanian, Upper Cretaceous) of Wiltshire, United Kingdom (Wright and Collins, 1972).

Discussion.—The type species of the genus is not particularly well known. None of the syntypes is well-preserved. They each lack cuticle over most of their surface, and most have at least portions of the margins broken.

XANTHOSIA ELEGANS Roberts, 1962
Figure 4.4

Xanthosia elegans ROBERTS, 1962, p. 177, pl. 89, figs. 1, 3. BISHOP, 1985, p. 622; BISHOP, 1991, p. 310; SCHWEITZER HOPKINS et al., 1999, p. 87, 88; GUINOT AND TAVARES, 2001, p. 516.

"*Xanthosia*" sensu lato *X. elegans* ROBERTS, 1962. SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace length about half maximum carapace width, maximum width about half the distance posteriorly; fronto-orbital width about half maximum carapace width; anterolateral margins with four or five small sharp spines including outer-orbital spines; cervical groove beginning along anterolateral margin about 37% the distance posteriorly, crossing midline about 55% the distance posteriorly.

Description.—Carapace wider than long, ovate, length about half carapace width, maximum width about half the distance posteriorly at position of last anterolateral spine; carapace flattened both transversely and longitudinally.

Front poorly known, about one-quarter maximum carapace width. Orbits shallow, directed forward, fronto-orbital width about half maximum carapace width. Anterolateral margins weakly convex, with four or five small, sharp spines including outer-orbital spine; anterolateral edges crispate, thin. Posterolateral margin sinuous, anteriorly convex, then concave. Posterior margin broadly concave, narrowly rimmed, about 40% maximum carapace width.

Mesogastric region with long anterior process, widened posteriorly; protogastric region about as wide as long, moderately inflated; hepatic regions wider than long; metagastric and urogastric regions confluent; cardiac region pentagonal, apex directed posteriorly; intestinal region flattened. Cervical groove beginning along anterolateral margin about 37% the distance posteriorly, arcing concave forward, then convex forward along base of inner hepatic region and base of protogastric region and arcing concave forward along base of

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FIGURE 2—Sternal architecture of members of Feldmanniidae (*1*, *2*, *4*) and Etyidae (*3*). *1*, *Feldmannia wintoni* (Rathbun, 1935), USNM 543681, female, oblique ventral view showing position of spermatheca on axial tip of sternite 7; *2*, oblique ventral view of *Caloxanthus americanus* Rathbun, 1935, USNM 543699, female, showing spermatheca as enlarged ovate opening on sternal suture 7/8; *3*, *4 Steorrosia pawpawensis* (Schweitzer Hopkins et al., 1999), USNM 543683, female, oblique ventral views showing spermatheca positioned entirely on sternite 7 and not as part of sternal suture 7/8, gonopore on coxa three positioned just anterior to spermatheca; *5*, *Feldmannia wintoni*, USNM 543682, male, oblique ventral view showing position of male gonopore on coxa 5 nearly on axial surface of coxa. G=gonopore, S=spermatheca. Scale bars=1 mm.

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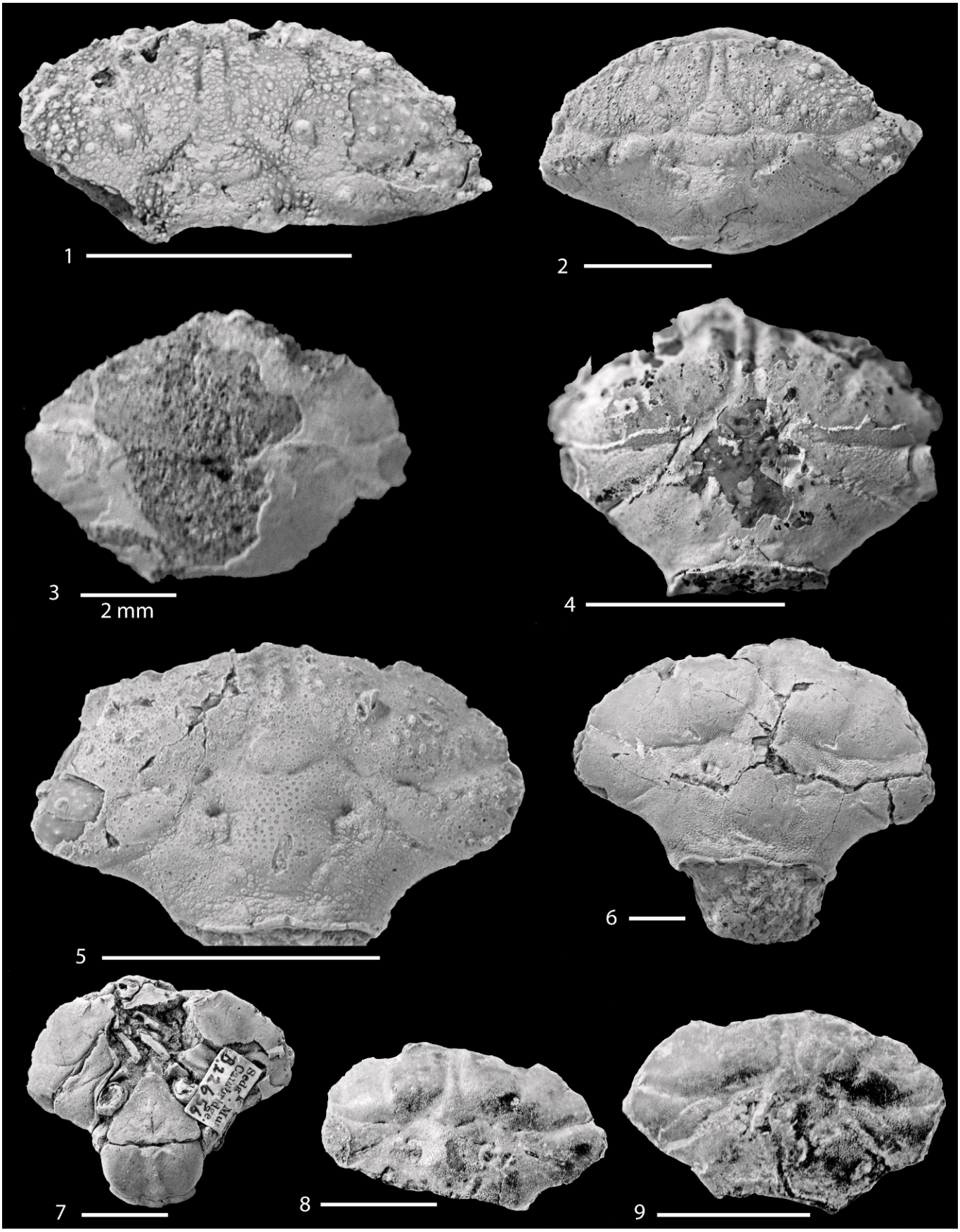

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mesogastric region, crossing midline about 55% the distance posteriorly. Branchiocardiac grooves developed as arcuate depressions along metagastric and urogastric regions.

Branchial regions subdivided into three distinct areas; epibranchial region composed of a distal area that embraces anterolateral spines 4 and 5, bounded anteriorly by cervical groove and posteriorly by bg1; mesobranchial region developed as a weak, more or less oblique ovate region bounded anteriorly by cervical groove, laterally by bg1, and axially by bg2; metabranchial region inflated anteriorly and flattened posteriorly.

Pereiopod 5 carried subdorsally. Pleonites 1–4 of female? pleon free, wider than long, widening distally.

Material examined.—NJSM GP22689.

Occurrence.—Merchantville Formation (lower Campanian), Maple Shade, New Jersey, U.S.A. (Roberts, 1962; Kennedy and Cobban, 1993); spoil piles on north side of Chesapeake and Delaware Canal in Delaware between routes 896 and 13, U.S.A. (Lauginiger, 1988), Merchantville and Marshalltown formations (middle to upper Campanian) (Wolfe, 1976).

Remarks.—The illustrated specimen retains cuticle that is eroded and leaves little trace of surface ornamentation. The original description of Roberts (1962) suggests that the surface may have been granular.

XANTHOSIA SEMIORNATA Jagt, Collins, and Fraaye, 1991
Figure 4.3

Xanthosia semiornata JAGT, COLLINS, AND FRAAYE, 1991, p. 556, fig. 3A–F. SCHWEITZER HOPKINS et al., 1999, p. 87, 88; GUINOT AND TAVARES, 2001, p. 517.

"*Xanthosia*" sensu lato *X. semiornata* JAGT et al., 1991. SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace widest about 60% the distance posteriorly; anterolateral margin convex, with five blunt triangular spines excluding outer-orbital margin, spines project anterolaterally; posterolateral margin straight, smooth; protogastric and hepatic regions with large ovate swellings; cervical groove beginning along anterolateral margin about half the distance posteriorly, extending weakly concave forward around base of hepatic region, then arcing weakly convex forward at lateral-most edge of protogastric region, then arcing concave forward around base of protogastric region, then arcing concave forward around base of mesogastric region crossing the midline about 60% the distance posteriorly on carapace.

Description.—Carapace wider than long, widest about 60% the distance posteriorly, length about half carapace width, weakly vaulted longitudinally, flattened transversely. Front about one-quarter maximum carapace width, nearly straight, weak axial notch and sulcus, terminating laterally in sharp corner. Orbital margin directed anterolaterally, upper orbital margin rimmed, with one fused fissure and two blunt upward directed projections; fronto-orbital width about two-thirds maximum carapace width. Anterolateral margin convex, with five blunt triangular spines excluding outer-orbital spines, spines project anterolaterally; posterolateral margin straight, smooth. Posterior margin half maximum carapace width, sinuous. Regions moderately defined by shallow grooves; mesogastric region broadens uniformly posteriorly, convex posterior margin, smooth; metagastric region wider than mesogastric region, smooth; urogastric region poorly defined, confluent with cardiac region; epigastric, protogastric and hepatic regions with large ovate swellings; protogastric and hepatic regions separated by shallow groove.

Cervical groove beginning along anterolateral margin about half the distance posteriorly, extending weakly concave forward around base of hepatic region, then arcing weakly convex forward at lateral-most edge of protogastric region, then arcing concave forward around base of protogastric region, then arcing concave forward around base of mesogastric region crossing the midline about 60% the distance posteriorly on carapace. Epibranchial regions ornamented with large ovate swellings, metabranchial region poorly defined, bounded axially by bg2, remainder of branchial region smooth.

Material examined.—Holotype, MAB k.0020.

Occurrence.—Late Cretaceous (Maastrichtian), The Netherlands.

Discussion.—*Xanthosia semiornata* shares several characters with the type species, including a relatively short anterolateral margin compared to the posterolateral margin, a cervical groove that begins rather far forward, some development of the oblique mesobranchial region on the carapace; a relatively wide front and fronto-orbital width, and spherical ornamentation. *Xanthosia semiornata* differs from the type species of *Xanthosia* in having a more sinuous cervical groove that follows a somewhat different path, in arcing concave forward before reaching the midline, and then arcing concave forward again around the midline, resulting in a scalloped appearance. The oblique branchial grooves and metabranchial region are much better developed on the type species and other species of *Xanthosia* than on *X. semiornata*. The anterolateral margins of *X. semiornata* have more spines of a somewhat different nature than do those of other species of *Xanthosia*. However, based upon the material at hand, *Xanthosia* seems to be the best placement for *X. semiornata* at this time.

GENUS ETYXANTHOSIA Fraaije, van Bakel, Jagt, and Artal, 2008

Type and sole species.—*Xanthosia fossa* Wright and Collins, 1972, by original designation and monotypy.

Diagnosis.—Carapace wider than long, about two-thirds as long as wide, widest about 60% the distance posteriorly; front broadly downturned (Fig. 5.3); deep orbits with two wide fissures and an intra-orbital spine (Fig. 5.3); four anterolateral spines including outer-orbital spine, spines large, rectangular at their bases, themselves spinose (Fig. 5.3); carapace regions with particularly large tubercles as ornamentation; protogastric and hepatic regions separated; relatively straight anterolateral margin, anterolateral margin about 80% length of posterolateral margin; epibranchial region bearing last anterolateral spine, separated from remainder of flattened branchial region by branchial groove, mesobranchial region directed at an angle and bounded by bg1 and bg2 moderately well developed (Fig. 5.4); sinuous posterolateral margin.

Material examined.—Holotype (BMNH) In.60996, paratypes (BMNH) 60995, 60997, all from the Cenomanian of U.K.; OUM

←

FIGURE 3—Etyidae, *Etyus* spp. *1*, *Etyus martini* Mantell, 1844, dorsal carapace, KSU D 1751; *2*, *E. martini*, KSU D 1516, cast of J.S.H.Collins Collection specimen 2367j; *3*, *Etyus jacksoni* (Wright and Collins, 1972), unwhitened holotype, (BMNH) In.60957; *4*, *Etyus buteonis* (Wright and Collins, 1972), unwhitened holotype, (BMNH) In.60958; *5*, *Etyus similis* Bell, 1863, SM B22637; *6*, *7*, *Etyus granulosa* (M'Coy, 1854), SM B.22656, female, dorsal carapace (6) and ventral surface with pleon (7); *8*, *E. granulosa*, unwhitened specimen, (BMNH) In.29736; *9*, *E. granulosa*, unwhitened specimen, (BMNH) In.29920–1. Scale bars=1 cm.

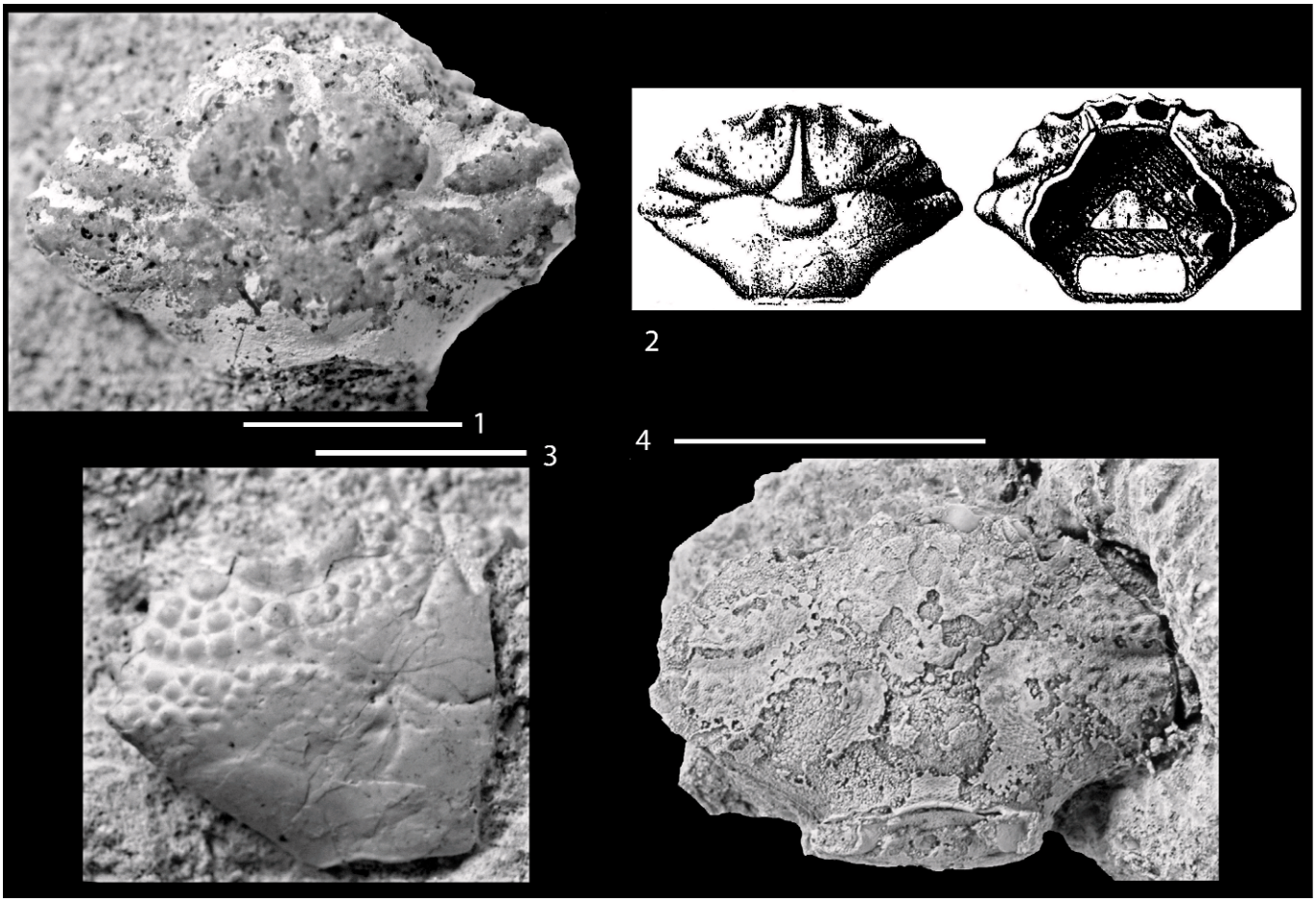

FIGURE 4—Etyidae, *Xanthosia* Bell, 1863 sensu stricto. *1*, *Xanthosia gibbosa* Bell, 1863, type species, (BMNH) 36647, syntype, unwhitened; *2*, *Xanthosia fischeri* (A. Milne-Edwards, 1862), digital image of A. Milne-Edwards (1862, plate 7, fig. 3); *3*, *Xanthosia semiornata* (Jagt et al., 1991), holotype, MAB k.0020, unwhitened; *4*, *Xanthosia elegans* Roberts, 1962, NJSM GP22689, whitened specimen. Scale bars=1 cm except 4.2 which A. Milne-Edwards (1862) reported as being "natural size;" we have reproduced the image at the same size as the original publication.

K.51634, Cenomanian of U.K.; MAB k.2571, k.2573, Albian–Cenomanian of Koskobilo quarry, Spain (A. Klompmaker).

Discussion.—Fraaije et al. (2008) erected *Etyxanthosia* to accommodate *Xanthosia fossa,* which was designated as the type species, as well as three species of *Xanthosia* known from Texas, *X. aspera, X. pawpawensis*, and *X. reidi*. As will be discussed later, these latter three species belong to a different genus.

Fraaije et al. (2008) appear to have diagnosed *Etyxanthosia* and the type species, *E. fossa*, primarily based upon the paratypes of *Xanthosia fossa*, illustrated in Wright and Collins (1972, pl. 20, figs. 5, 6a, 6b), as well as a specimen from the Albian–Cenomanian of Spain that they illustrated (Fraaije et al., 2008, pl. 2, fig. 4). The holotype of *X. fossa* is quite incomplete; it is poorly preserved, an internal mold lacking cuticle (Wright and Collins, 1972, pl. 20, figs. 4–6), and it has been coated with blue paint. The description of the genus and species in Fraaije et al. (2008) mentioned a broad, downturned rostrum which is not visible in any of the paratypes or the holotype, nor is it visible in the illustration provided in Fraaije et al. (2008). They also described the mesobranchial region as possessing posterolateral spines which we are unable to confirm in any published illustrations. However, examination of a specimen from a locality near to that of the Fraaije et al. (2008) specimen indicates that the front is indeed extremely broad and downturned and that the last anterolateral spine is large and is itself spinose, accounting for the spines described as occurring on the mesobranchial region (Fig. 5.3).

By careful comparison of MAB k.2571 and 2573 to the holotype and other specimens referred to *Xanthosia fossa*, we conclude that all of the mentioned specimens in this discussion are indeed *X. fossa*, although the species is rather variable. For example, the cervical groove in the Fraaije et al. (2008) specimen is nearly straight laterally, whereas that of both the holotype and paratypes is concave laterally. The ornamentation described as ridges on the protogastric region by Fraaije et al. (2008) appear to us as large tubercles of varying size and habit, depending on the specimen examined. The Fraaije et al. (2008) specimen as well as the specimens we examined were collected from different localities than the type material, which could easily account for differences among the members of the species.

Fraaije et al. (2008, p. 199) differentiated *Etyxanthosia* from *Xanthosia* by *Etyxanthosia* having small orbits, a smaller fronto-orbital width, well-developed carapace regions, a downturned front, radially arranged ridges and/or tubercles on the protogastric region, and spines on the posterolateral margin. Examination of the specimens of *E. fossa* from the Koskobilo locality (Fig. 5.3, 5.4) suggests that their fronto-orbital width to width ratio is the same as the type species of *Xanthosia*; the orbits are poorly known in the type species of *Xanthosia*. The orbits of *Etyxanthosia fossa* are distinctive in being deep, with two deep, open fissures and a sharp spine between the fissures.

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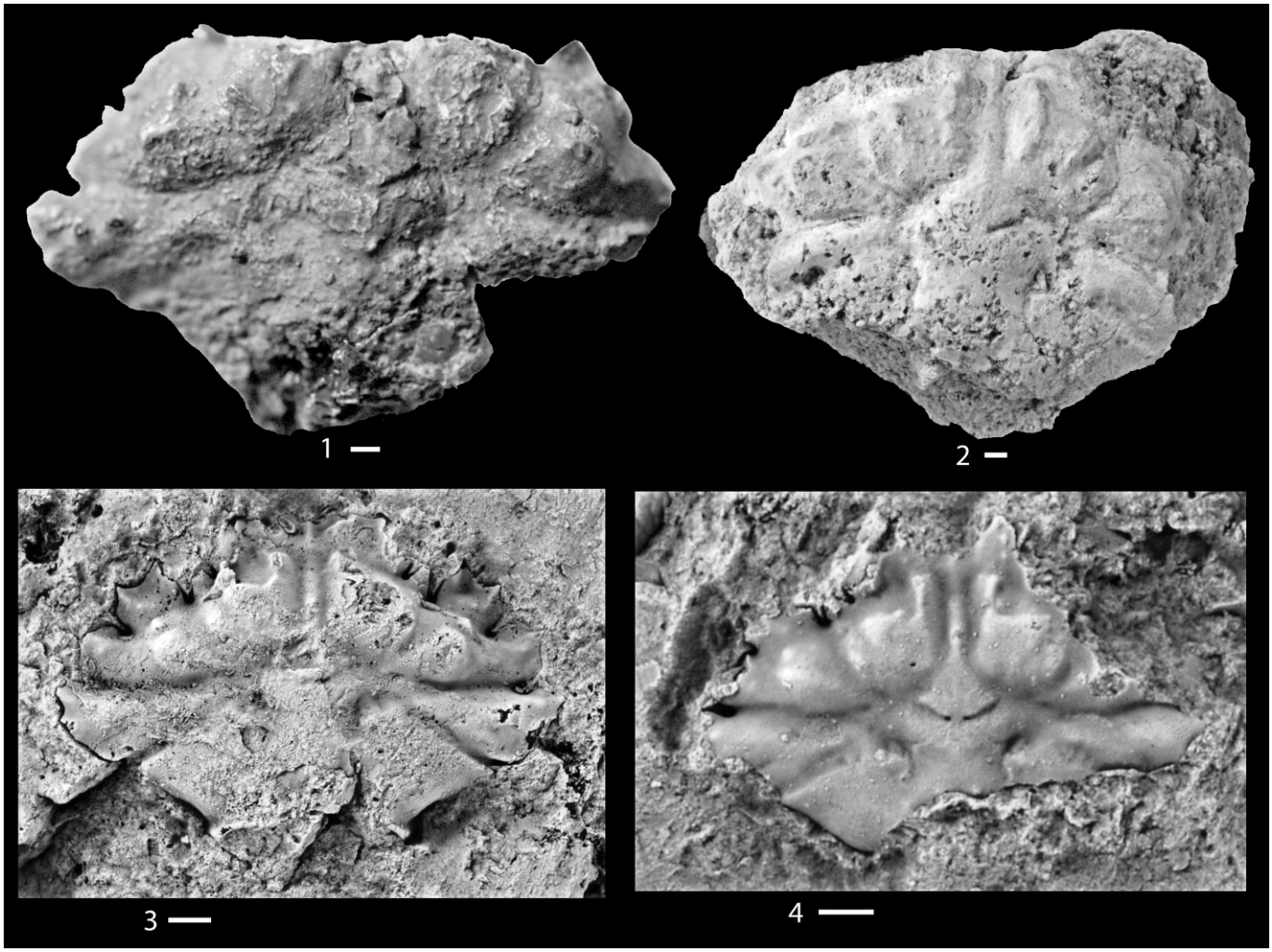

FIGURE 5—Etyidae, *Etyxanthosia fossa* (Wright and Collins, 1972). *1*, (BMNH) In.60996, holotype; *2*, OUM K.51634, partial dorsal carapace showing ridge-like ornamentation on protogastric region; *3*, MAB k.2571, well preserved specimen showing broad, downturned front; intra-orbital spine; and broad, highly ornamented anterolateral spines; *4*, MAB k.2573, moderately preserved specimen showing oblique mesobranchial region, bg1, and bg2. Scale bars=1 mm.

The front is poorly known on other species that have been referred to *Xanthosia*, so it is unknown as to whether other species may have similar fronts to *Etyxanthosia fossa*. The posterolateral margin of *Etyxanthosia fossa* does not seem to have spines; the spines described as posterolateral seem to be spines ornamenting the large last anterolateral spine itself. The posterolateral margin is itself not spinose. The main points of differentiation between *Etyxanthosia* and other genera within the family are possession of only four anterolateral spines including the outer-orbital spine, with these spines being large and rectangular at their bases and themselves spinose; deep orbits with clear fissures and an intra-orbital spine; particularly large tubercles as ornamentation; a relatively straight anterolateral margin; and a sinuous posterolateral margin. No other genus possesses this combination of characters. In fact, *E. fossa* is the only species at this time with this combination of features.

ETYXANTHOSIA FOSSA (Wright and Collins, 1972)
Figure 5

Xanthosia fossa WRIGHT AND COLLINS, 1972, p. 100, pl. 20, figs. 4–6.

Etyxanthosia fossa (WRIGHT AND COLLINS, 1972). FRAAIJE et al., 2008, p. 199; SCHWEITZER et al., 2010, p. 67.

Diagnosis.—Carapace wider than long, about two-thirds as long as wide, widest about 60% the distance posteriorly; front broadly downturned (Fig. 5.3); deep orbits with two wide fissures and an intra-orbital spine (Fig. 5.3); four anterolateral spines including outer-orbital spine, spines large, rectangular at their bases, themselves spinose (Fig. 5.3); carapace regions with particularly large tubercles as ornamentation; protogastric and hepatic regions separated; relatively straight anterolateral margin, anterolateral margin about 80% length of posterolateral margin; epibranchial region bearing last anterolateral spine, separated from remainder of flattened branchial region by branchial groove, mesobranchial region directed at an angle and bounded by bg1 and bg2 moderately well developed (Fig. 5.4); sinuous posterolateral margin.

Description.—Carapace transversely ovate, wider than long, length about two-thirds maximum width, widest at position of last anterolateral spine about 60% the distance posteriorly. Front broadly downturned; deep orbits with two wide fissures and an intra-orbital spine; fronto-orbital width about 60% maximum carapace width (Fig. 5.3). Anterolateral margin with four spines including outer-orbital spine, spines large, rectangular at their bases, themselves spinose; outer-orbital spine directed forward; first and second anterolateral spine directed

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anterolaterally; last anterolateral spine large, fan-shaped, with spinelets on it wrapping all around so that some spinelets are directed posterolaterally; anterolateral margin about 80% length of posterolateral margin (Fig. 5.3). Posterolateral margin sinuous. Posterior margin broadly concave, narrowly rimmed.

Mesogastric region widened posteriorly, narrowing into elongate anterior extension; metagastric and urogastric regions poorly distinguished from one another, urogastric slightly more depressed than metagastric; cardiac region ovate; regions with particularly large tubercles as ornamentation; protogastric and hepatic regions separated; epibranchial region bearing last anterolateral spine, separated from remainder of flattened branchial region by branchial groove, mesobranchial region directed at an angle and bounded by bg1 and bg2 moderately developed (Fig. 5.4); sinuous posterolateral margin. Cervical groove beginning between third and fourth anterolateral spine about 54% the distance posteriorly, extending either straight or concave forward across carapace.

Ventral surface and appendages unknown.

Occurrence.—This species ranges from the Albian–Cenomanian of Spain to the Cenomanian of the U.K.

Remarks.—The description for the species is based upon all of the known specimens. It is considerably expanded here as compared to the original description (Wright and Collins, 1972).

GUINOTOSIA Beschin, Busulini, De Angeli, and Tessier, 2007

Type species.—*Guinotosia tertiaria* Beschin, Busulini, De Angeli, and Tessier, 2007, by original designation and monotypy.

Diagnosis.—Carapace wider than long; front appearing to have six lobes, downturned; anterolateral margin appearing to have large triangular spines with rectangular bases; posterolateral margin sinuous; posterior margin weakly concave; protogastric region well-separated from hepatic region; hepatic region subdivided; cervical groove overall concave forward, beginning along anterolateral margin about half the distance posteriorly, crossing midline 66% the distance posteriorly; epibranchial region with 2 large anterolateral spines on margin; oblique mesobranchial region bounded by well-defined bg1 and bg2; carapace regions appear to have been well-ornamented.

Occurrence.—Eocene (Ypresian) of Italy (Beschin et al., 2007).

Discussion.—*Guinotosia* is referrable to Etyidae based upon its possession of an oblique mesobranchial region bounded by bg1 and bg2 and an epibranchial region with anterolateral spines with rectangular bases and triangular tips. The development of carapace regions is similar to that seen in other etyids such as *Xanthosia*, *Steorrosia*, and *Etyus*. *Guinotosia* differs from other etyids in having a cervical groove that is overall concave forward instead of having a sinuous path. *Guinotosia* is one of the few etyids with a preserved front; it, like that of *Etyxanthosia*, suggests that the fronts are wide and spinose in this family.

Genus STEORROSIA new genus

Type species.—*Xanthosia aspera* Rathbun, 1935, p. 41, by designation herein.

Included species.—*Steorrosia aspera*; *Steorrosia pawpawensis* (Schweitzer Hopkins et al., 1999); *Steorrosia reidi* (Schweitzer Hopkins et al., 1999).

Diagnosis.—Carapace much wider than long, length about half carapace width, position of maximum width at 50–75% maximum carapace length; carapace regions moderately to well defined by grooves and ornamented by tubercles of varying sizes; front poorly known, appearing to have been nearly straight, not extending much beyond orbits, fronto-orbital width about 40% maximum carapace width (Fig. 6.3); anterolateral margins with between five and seven larger spines and may have smaller tubercles interspersed between them or ornamenting larger spines, spines may be small and sharp or large and rectangular at bases, anterolateral margin broadly convex; posterolateral margin concave; axial regions with three large tubercles in longitudinal row; epibranchial region composed of a distal area that embraces last anterolateral spines bounded anteriorly by cervical groove and posteriorly by bg1; mesobranchial region developed as a more or less oblique ovate region bounded anteriorly by cervical groove, laterally by bg1, and axially by bg2; metabranchial region flattened. Cervical groove beginning along anterolateral margin about 35% the distance posteriorly, arcing concave forward, then convex forward at base of protogastric region, then concave forward around base of mesogastric region about 50% the distance posteriorly (Fig. 6.1).

Female sternum narrow (Fig. 2.3, 2.4), deep; sternites 1–3 fused, triangular, separated from sternite 4 by grooves; sternite 4 with rectangular anterior process, pereiopod 1 articulating at intersection between anterior process and episternal projection which is directed laterally and upward at about 45° angle to flat sternal cavity; sternite 5 with large episternal projections directed laterally and upward at about 45° angle to flat sternal cavity, articulating with pereiopod 2; sternite 5 and 6 separated by complete suture; sternite 6 with episternal projections directed posterolaterally, articulating with pereiopod 3; sternites 7 and 8 directed strongly posterolaterally, wider than long, 8 longer than 7; external opening of spermatheca situated entirely on sternite 7, apparently not as part of suture between 7 and 8 (Fig. 2.3, 2.4), transversely ovate, surrounded with granules, anterior and axial edge of sternite 7 raised and rotated ventrally; anterior end of sternite 8 overlapping posterior end of sternite 7 (Fig. 2.4).

Pleon wide in both males and females; all pleonites free. Female pleonites wide, covering part of coxae of pereiopods; pleonites 1–6 with axial swellings; coxae 1–5 with lateral swellings; pleonites with depressed rim along posterior margin; pleonite 6 twice as long as other pleonites; telson locking into coxae of pereiopods 1, with longitudinal groove; posterior margin of pleonites sinuous, with posteriorly directed projection axially. Male pleon similar in form to female but narrower and flatter.

Third maxillipeds longer than wide; in two planes (Fig. 6.2, 6.3). Pereiopods decreasing in size posteriorly; coxae of pereiopod 1 with abdominal locking mechanism; coxae of pereiopod 3 with female gonopores, gonopores situated on ventral surface and close to sternal edge of coxa, position of gonopores just anterior to spermatheca; pereiopod 5 carried at least subdorsally and possibly fully dorsally, reduced in size compared to other pereiopods (Figs. 6.1, 7.1).

Etymology.—The genus name is derived from the Anglo-Saxon root *steorra*, meaning starry, referring to the location of all three species of the genus in the American state of Texas, referred to as the Lone Star State. The ending –osia reflects a common ending for genera within the family. The gender is feminine.

Material examined.—*Steorrosia aspera*, USNM 543680; *S. pawpawensis*, USNM 643683, 543690–93; *S. reidi*, USNM 543697–8, in addition to numerous (hundreds) of unnumbered specimens of all three species from the Robert Reid collection currently under study by one of the current authors (OF).

Occurrence.—The three species of *Steorrosia* range in age from Albian (Early Cretaceous) to Cenomanian (Late

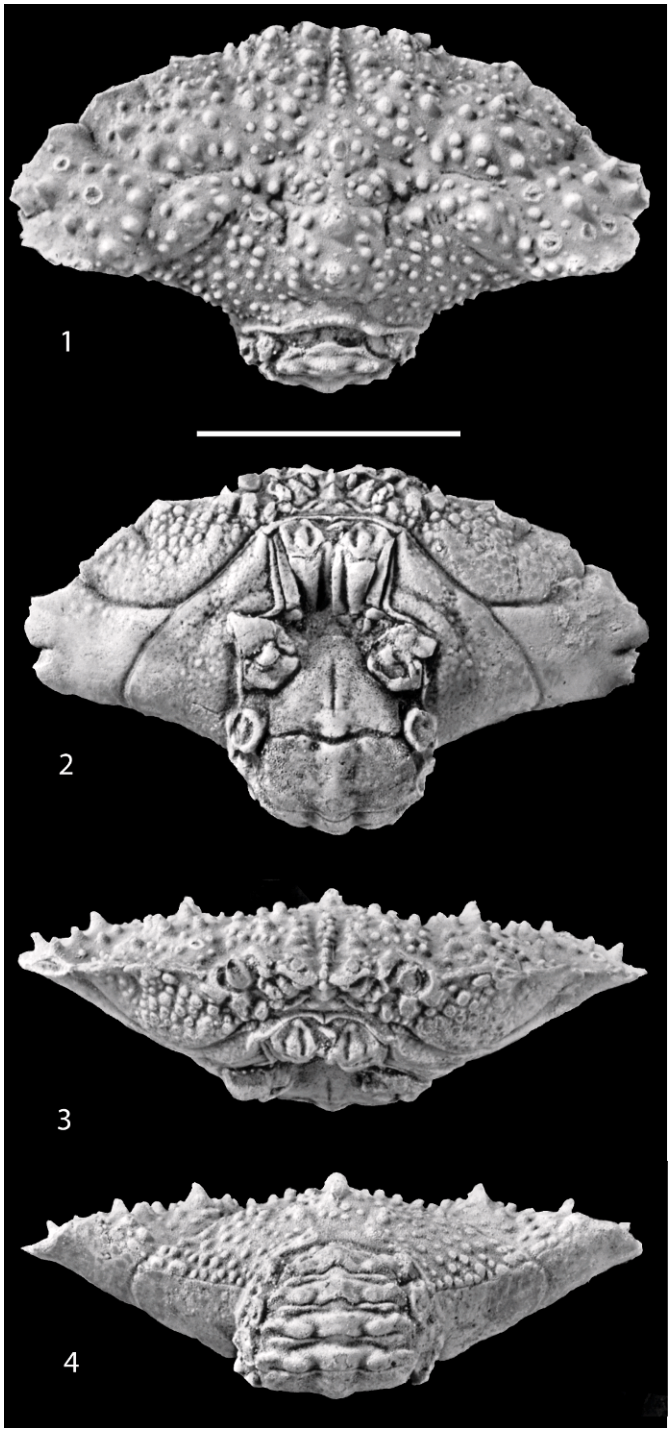

FIGURE 6—Etyidae, *Steorrosia aspera* (Rathbun, 1935), USNM 543680, female, dorsal (*1*), ventral (*2*), anterior (*3*), and posterior (*4*) views. Scale bar=1 cm.

Cretaceous) (Schweitzer Hopkins et al., 1999) from numerous localities (Table 1).

Discussion.—*Steorrosia* differs from all other genera within Etyidae in possessing a combination of narrow frontoorbital width compared to the maximum carapace width; a much stronger oblique mesobranchial region than other genera; and a more spinose anterolateral margin (Figs. 6, 7).

Fraaije et al. (2008, p. 199) originally placed the three species here referred to *Steorrosia* into *Etyxanthosia* based upon their small orbits, narrow fronto-orbital width as compared to the total width of the carapace; anterolateral margins with spines; radial ridges or tubercles on the protogastric region; a downturned front; spines on the posterolateral margin; and well-defined carapace regions. In fact, the three species of *Steorrosia* have narrow fronto-orbital widths as compared to the total width, and it is one of the defining characteristics of the genus. However, the type species of *Etyxanthosia* has a fronto-orbital width that is wide and is about the same as compared to the total width as that of *Etyus* spp. and *Xanthosia* spp. Further points of difference between *Steorrosia* spp. and *Etyxanthosia* include short front in *Steorrosia* which gives no evidence of extending much beyond the orbits; lack of radial ridges or tubercles on the protogastric region in *Steorrosia*; a cervical groove that begins much further anteriorly (35% the distance posteriorly in *Steorrosia* as compared to 54% in *Etyxanthosia*); and possession of many more anterolateral spines (four in *Etyxanthosia* vs. five to seven in *Steorrosia*). Thus, the two genera are easily differentiated.

Schweitzer Hopkins et al. (1999) separated the material from Texas into three different species based upon ornamentation, the nature of the anterolateral margins, and development of regions. Examination of hundreds of additional specimens from the Pawpaw Formation indicates that this division appears to hold; the separation does not appear to be related to gender, size, or age.

GENUS SECRETANELLA Guinot and Tavares, 2001

Type species.—*Xanthosia arcuata* Secretan, 1964, by original designation and monotypy.

Included species.—*Secretanella arcuata*; *S. buchii* (Reuss, 1845), provisionally; *S. occidentalis* (Bishop, 1985); *S. socialis* (van Bakel et al., 2005) provisionally; *S. spinosa* (Bishop, 1991).

Diagnosis.—Carapace wider than long, length 55–60% maximum carapace width, widest about half the distance posteriorly on carapace at position of last anterolateral spines; carapace flattened transversely and longitudinally; fronto-orbital width 50–60% maximum carapace width; anterolateral margins convex, with five to seven small, sharp spines (Fig. 8.1); posterior margin narrow, 25–35% maximum carapace width; cervical groove beginning 45–50% distance along anterolateral margin, curving concave forward for about half width of hepatic region, then strongly convex forward until base of mesogastric region, where it curves concave forward across midline about 50–60% the distance posteriorly on carapace; branchial region inflated posterior to convex forward segment of cervical groove; oblique bg1 and sometimes mesobranchial region present (Fig. 8.1, 8.4); sternites poorly preserved, appearing to have a complete sternal suture 5/6 (Fig. 8.3); sternites anterior to suture with laterally directed episternites; sternites posterior to suture directed posterolaterally; female pleon wide, first and second pleonites narrow, pleonites widening toward broadly rounded telson, extending to anterior of sternite 4 and beyond coxae of pereiopods 1 (Fig. 8.5, 8.6).

Material examined.—*Secretanella arcuata*, MNHN R03978, holotype; MNHN R03980, paratype; MNHN A31661, paratype.

Occurrence.—Cenomanian (Late Cretaceous) of Madagascar; lower Campanian rocks of Münsterland, Germany; Campanian (Late Cretaceous) of Colorado, South Dakota, U.S.A.

Discussion.—Guinot and Tavares (2001) recognized that *Xanthosia arcuata* differed from other species of *Xanthosia* and therefore placed it within a new genus, *Secretanella*, within the Heterotremata. However, *Secretanella arcuata* (Fig. 8.4) possesses the oblique bg1 and mesobranchial region, sinuous cervical groove, wide female pleonites, spinose anterolateral margin, and wider than long carapace typical of the Etyidae, in which we place it.

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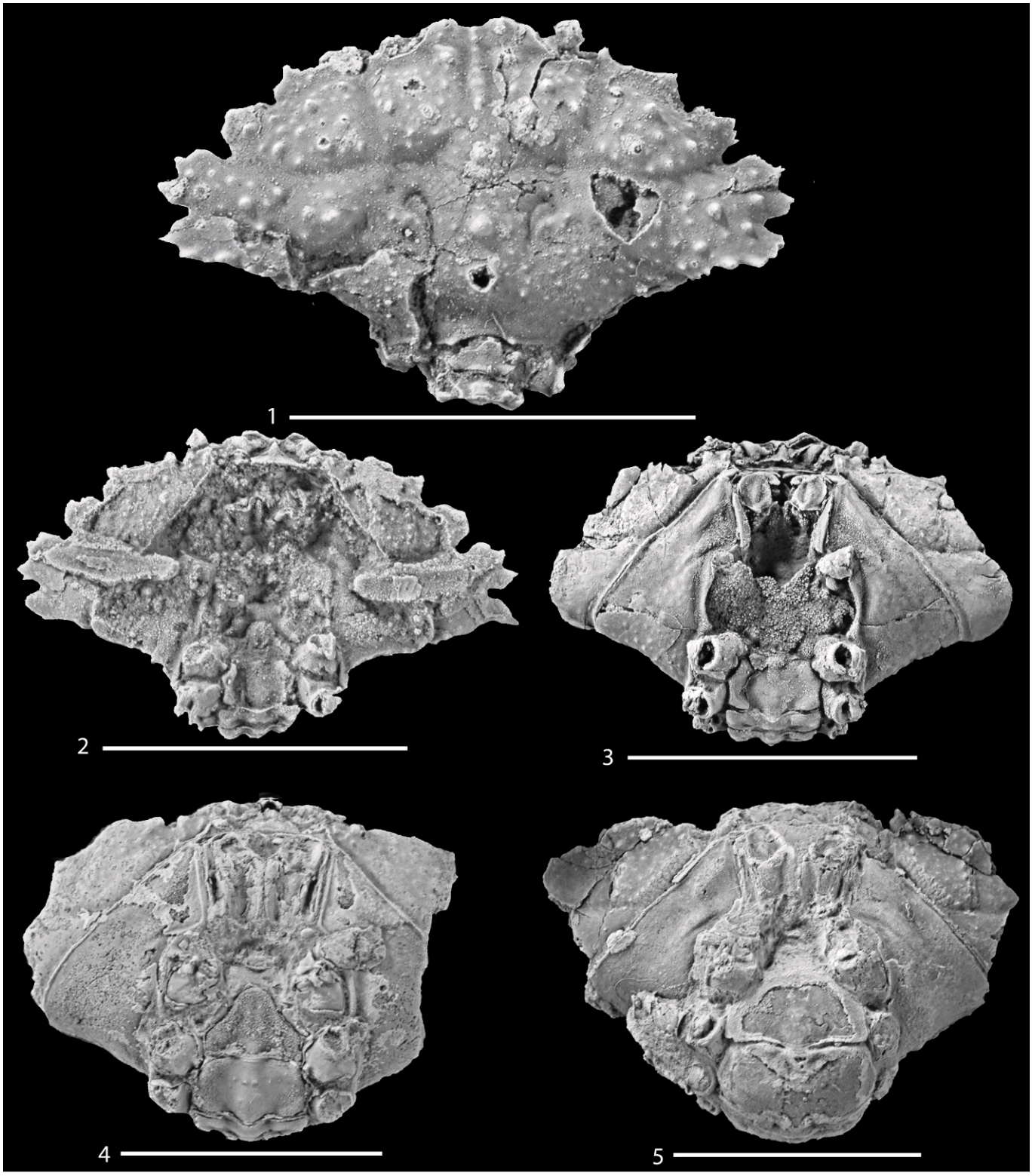

FIGURE 7—Etyidae, *Steorrosia pawpawensis* (Schweitzer Hopkins et al., 1999). *1*, *2*, USNM 543690, male, dorsal carapace (1) and (2) male sternum and pleon; *3*, USNM 543691, female sternum and pleon; *4*, USNM 543692; female pleon; *5*, USNM 543693, mature female pleon. Scale bars=1 cm.

Bishop (1985, 1991) described two species of *Xanthosia* from Upper Cretaceous rocks of the Western Interior Seaway, U.S.A. These two species are referable to Etyidae based upon their possession of an arcuate and sinuous cervical groove, an oblique bg1, and sternal elements that appear similar to those of *Steorrosia*. They differ from *Xanthosia*, *Steorrosia*, and *Etyus* in lacking a well-developed oblique mesobranchial region, and in possessing six or seven anterolateral spines, weakly developed carapace regions, a much narrower posterior margin, and a much more arcuate cervical groove. In fact, their features are similar to *Secretanella*, especially the possession of an arcuate cervical groove and an inflated area

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TABLE 1—Localities for specimens of *Steorrosia* spp., *Feldmannia wintoni*, and *Caloxanthus americanus*.

Locality	*Steorrosia pawpawensis*	*Steorrosia aspera*	*Steorrosia reidi*	*Feldmannia wintoni*	*Caloxanthus americanus*
Dirk's Site N 32°37′48.40″ W 97°24′29.81″	0	23 USNM 543680	0	1	6 USNM 543694–96
Browning Site N 32°50′57.50″ W 97°14′53.16″	516 USNM 543683, 90–94	0	0	251 USNM 543684–89	1
Motorola N 32°50′48.63″ W 97°17′13.51″	4	0	6 USNM 543697–98	1	1
Harmon N 32°55′29.00″ W 97°19′31.60″	0	11	0	4	0
Nursing Home N 32°46′10.77″ W 97°14′36.24″	13	0	0	3	0
Haslet N 32°57′27.77″ W 97°18′32.52″	0	3	0	6	0
Walmart N 32°50′34.94″ W 97°14′51.50″	29	0	0	19	0
I-35S N 32°38′49.41″ W 97°19′42.16″	0	7	0	0	11
Renfro Loc. #12 7/8 miles east of Watagua, North of Fort Worth, TX	N/A	N/A	N/A	7 USNM 543681–82	N/A

posterior to the cervical groove. Thus, we place these species within *Secretanella*.

The genus has a rather disjunct distribution in time and space. The oldest species is *Secretanella arcuata* from the Cenomanian of Madagascar. The remaining species are Campanian in age from North America and Europe.

SECRETANELLA OCCIDENTALIS (Bishop, 1985)
Figure 8.1–8.3

Xanthosia elegans occidentalis BISHOP, 1985, p. 622, figs. 3, 6, 13.

Xanthosia occidentalis BISHOP, 1985. BISHOP, 1991, p. 307, figs. 1i, 2, 3, 6; SCHWEITZER HOPKINS et al., 1999, p. 87, 88; GUINOT AND TAVARES, 2001, p. 516.

"*Xanthosia*" sensu lato *X. occidentalis* BISHOP, 1991. SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace wider than long, length about 54% maximum carapace width, widest about 40% the distance posteriorly on carapace at position of last anterolateral spines; carapace flattened transversely and longitudinally; fronto-orbital width half maximum carapace width; anterolateral margins convex, with six small, sharp spines; posterior margin narrow, 35% maximum carapace width; cervical groove beginning about 45% the distance along anterolateral margin, curving concave forward for about half the width of hepatic region, then strongly convex forward to base of mesogastric region, where it curves concave forward across midline about 60% the distance posteriorly on carapace; branchial region inflated posterior to convex forward area; oblique bg1 present; sternites poorly preserved, appearing to have complete sternal suture 5/6; sternites anterior to suture with laterally directed episternites; sternites posterior to suture directed posterolaterally.

Description.—Carapace wider than long, ovate, length about 54% carapace width, position of maximum width about 40% the distance posteriorly on carapace at position of last anterolateral spines; carapace flattened both transversely and longitudinally.

Front poorly known. Orbits forward directed, with two open fissures, fronto-orbital width about 45% maximum carapace width. Anterolateral margin with about six spines, spines small, sharp; last two longer, attenuated, needle-like; entire margin weakly convex. Posterolateral margin weakly convex; posterior margin narrow, concave, about 35% maximum carapace width.

Regions weakly defined on cuticular surface, much better defined on molds of interior, yielding very different appearance depending on which is examined. Mesogastric region narrow, widened somewhat posteriorly; metagastric and urogastric regions confluent, urogastric region narrow, depressed; cardiac region inflated, pentagonal, on interior molds, with two or three small tubercles. Protogastric regions about as wide as long; hepatic regions about twice as wide as long. On cuticular surface, branchial regions not differentiated; on molds of interior, epibranchial region defined axially by weak, oblique bg1 and laterally by anterolateral margin embracing spines 5 and 6.

Cervical groove beginning about 45% the distance along anterolateral margin, curving weakly concave forward for about half the width of hepatic region, then strongly convex forward to base of mesogastric region, where it curves concave forward across midline about 60% distance posteriorly on carapace; branchial region inflated posterior to convex forward area.

Sternites poorly preserved, appearing to have complete sternal suture 5/6; sternites anterior to suture with laterally directed episternites; sternites posterior to suture directed posterolaterally.

Material examined.—SDSM 10036, holotype; SDSM 10037, paratype; topotypes SDSMT 880801, 86605–86608.

Occurrence.—Gammon Ferruginous Member, Pierre Shale, Campanian (Late Cretaceous), South Dakota (Bishop, 1991).

Discussion.—Several topotypes from the South Dakota School of Mines and Technology add considerably to the original description (Bishop, 1991). These specimens retain some portions of the sternites, which indicate similarities with those of *Steorrosia* spp., one of the main bases upon which we

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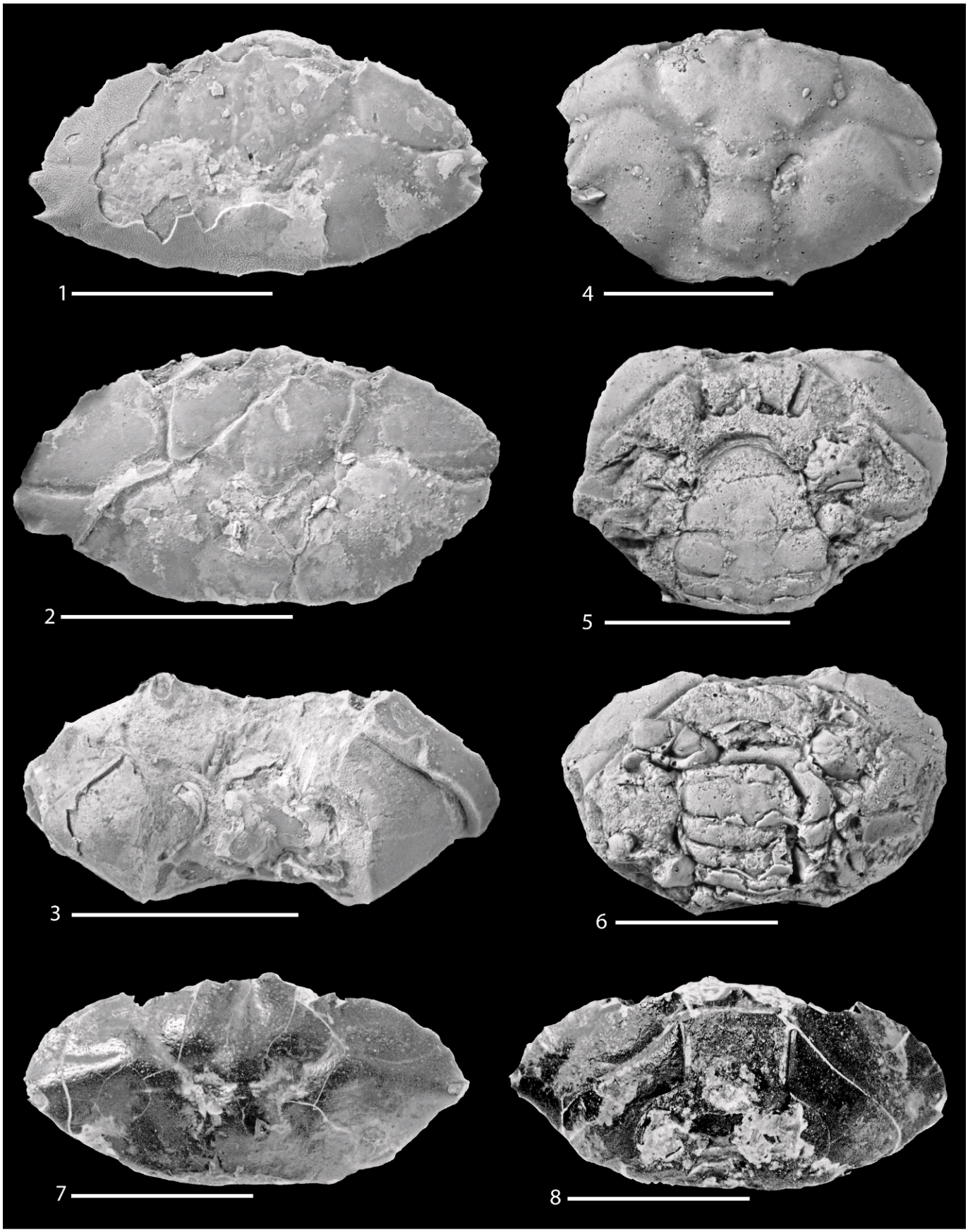

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refer this genus to Etyidae. The topotypes also indicate that the species exhibits quite different morphologies when cuticle is preserved as compared to when the cuticle is exfoliated and molds of the interior are examined.

Secretanella spinosa (Bishop, 1991)

Xanthosia spinosa Bishop, 1991, p. 311, fig. 4. Schweitzer Hopkins et al., 1999, p. 87, 88; Guinot and Tavares, 2001, p. 516.

"*Xanthosia*" sensu lato *X. spinosa* Bishop, 1991; Schweitzer et al., 2010, p. 131.

Diagnosis.—Carapace wider than long, length about 60% maximum carapace width, widest at position of sixth anterolateral spine, about 55% the distance posteriorly; anterolateral margins tightly convex, with seven spines including outer-orbital spines; front with four spines including inner-orbital spines; orbits shallow, directed forward; cervical groove beginning along anterolateral margin between spines 5 and 6 about 50% the distance posteriorly, arcing strongly concave forward, for about half the width of the hepatic region, then strongly convex forward, then concave forward around base of mesogastric region about half the distance posteriorly; mesobranchial region weakly developed, oblique, bg1 and bg2 weak; posterior margin narrow, about 25% maximum carapace width.

Material examined.—The holotype, UCMG 30375, has been reported to be missing (T. Karim, UCMG, personal communication, January 2011).

Occurrence.—Campanian (Late Cretaceous) of Colorado, U.S.A.

Discussion.—*Secretanella spinosa* differs from *S. occidentalis* in possessing more anterolateral spines on a more tightly convex margin, a more sinuous cervical groove, and appearing to have an oblique mesobranchial region. However, the latter may be an illusion on the illustration in Bishop (1991), and since the type seems to be lost, we must await better preserved material to determine if this feature is truly present.

Secretanella? buchii (Reuss, 1845)
Figure 8.7, 8.8

Podophthalmus buchii Reuss, 1845, p. 15, pl. 5, fig. 50.

Reussia buchii (Reuss). M'Coy, 1854a, p. 271; M'Coy, 1854b, p. 121; Reuss, 1859, p. 8, pl. 2, fig. 4; A. Milne-Edwards, 1862, p. 79, pl. 5, fig. 3.

Etyus buchii (Reuss). A. Milne-Edwards, 1865, p. 347; Fritsch and Kafka, 1887, p. 48, text-figure 70; Fritsch, 1893, p. 105, fig. 132.

Xanthosia buchii (Reuss). Glaessner, 1929, p. 401; Wright and Collins, 1972, p. 97; Schweitzer et al., 2010, p. 67.

Diagnosis.—Carapace wider than long, widest at midlength, weakly vaulted longitudinally, flattened transversely; regions poorly defined; orbits circular, directed forward, upper orbital margins with at least one fissure; anterolateral margin with four tiny spines and one larger, laterally directed anterolateral spine excluding outer-orbital spine; posterolateral margin appearing to have been sinuous, entire. Mesogastric region elongate, triangular; protogastric regions large, inflated; hepatic region depressed; metagastric region poorly defined; cardiac region pentagonal, inflated. Cervical groove concave forward, arising anterior to fourth anterolateral spine, concave forward around base of protogastric and mesogastric regions; gastric muscle scars posterior to cervical groove; epibranchial region a transversely elongate ridge extending from anterolateral corner to axis, arcing slightly anteriorly; remainder of branchial region undifferentiated.

Material examined.—NHMW 1864.XL.604, holotype.

Occurrence.—Turonian (Late Cretaceous) of the Plänermergel, Hochpetsch, Czech Republic. Glaessner (1929, p. 401) noted that Reuss's (1845) original consideration of the type locality as Hochpetsch was an illusion because the preservation style permitted the interpretation with certainty that the specimen was from the Cambridge Greensand. We are inclined to accept Reuss's original locality, as there are no specimens similar to *Xanthosia buchii* from among the many brachyurans known from the Cambridge Greensand.

Discussion.—The synonymy given above shows the difficulty in placement of this species. It is known from a single fragmentary specimen. Glaessner (1929) placed this species within *Xanthosia*. However, the path of the cervical groove, the crispate anterolateral margin, and the general arrangement of regions suggest that it is best placed within *Secretanella*. The distinct ridge on the epibranchial region makes it unlike any other taxon within Etyidae, including *Secretanella,* but the incomplete nature of the single specimen of this species makes it unwise to erect a new genus for it.

Secretanella? socialis (van Bakel et al., 2005)

Xanthosia socialis Van Bakel, Fraaije, and Jagt, 2005, p. 288, figs. 1, 2.

"*Xanthosia*" sensu lato *X. socialis* Van Bakel, Fraaije, and Jagt, 2005; Schweitzer et al., 2010, p. 131.

Diagnosis.—Carapace wider than long, length about 60% maximum carapace width, widest about half the distance posteriorly on carapace. Fronto-orbital width about 60% maximum carapace width, orbits forward directed, possibly with one short fissure; anterolateral margins appearing to be nearly straight, with a laterally directed spine at termination; posterolateral margins weakly convex, with a blunt spine at position of intersection of oblique metabranchial region with margin; posterior margin about 35% maximum carapace width, concave. Protogastric regions well-defined laterally; on internal mold; cervical groove beginning about 40% the distance posteriorly, apparently nearly straight laterally, then convex forward along most of length of hepatic region and protogastric region, arcing concave forward along base of mesogastric region and crossing midline about half the distance posteriorly. Oblique mesobranchial region weak, bg1 and bg2 weak.

Occurrence.—The holotype was collected from lower Campanian rocks of Münsterland, Germany (van Bakel et al., 2005).

Discussion.—This species was described and illustrated from a cast of what appears to be mostly a mold of the interior of the dorsal carapace, based upon the lack of ornamentation on the mold. The carapace margins are poorly known and

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Figure 8—Etyidae, *Secretanella* spp. *1*, *Secretanella occidentalis* (Bishop, 1985), SDSM 880801, topotype; *2*, *S. occidentalis*, SDSMT 86607, topotype; *3*, *S. occidentalis*, ventral surface, SDSMT 86608, topotype; *4*, *S. arcuata* (Secretan, 1964), cast of MNHN R03978, holotype, KSU D1294; *5*, *S. arcuata*, ventral surface of female pleon, cast of MNHN A31661, paratype, KSU D1296; *6*, *S. arcuata*, ventral surface of female pleon, cast of MNHN R03980, paratype, KSU D1295; *7*, *8*, *S. buchii* (Reuss, 1845), NHMW 1864.XL.604, holotype, dorsal carapace (7) and ventral surface (8), unwhitened. Scale bars=1 cm.

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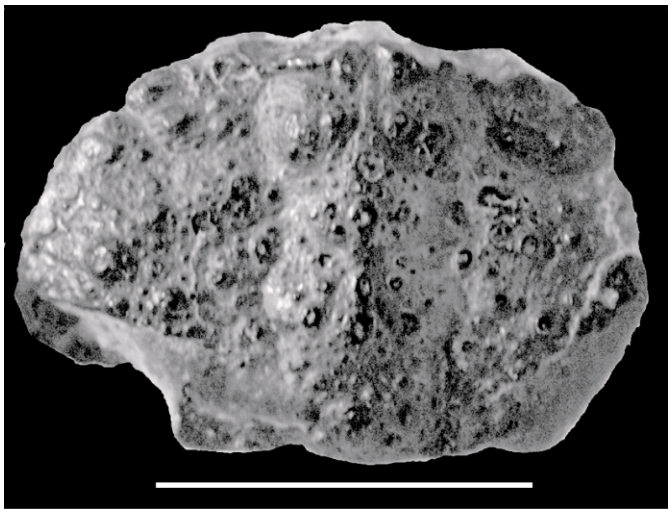

FIGURE 9—Etyidae, *Sharnia burnhamensis* Collins and Saward, 2006, (BMNH) IC.454, holotype, unwhitened. Scale bar=1 cm.

illustrated; thus, the ratios for the carapace reported here are based upon the illustrations. It is difficult to determine from the illustration whether or not the right anterolateral margin is fully exposed or continues below the sediment. At this time, the best placement for this species seems to be *Secretanella*, based upon the path of the cervical groove and the poorly developed mesobranchial region and bg1 and 2 in this species. Specimens with more complete and better preserved margins might help to confirm this placement.

GENUS SHARNIA Collins and Saward, 2006

Type species.—*Sharnia burnhamensis* Collins and Saward, 2006, by original designation and monotypy.

Diagnosis.—Carapace wider than long, widest near anterolateral corner; anterolateral margin crispate, spined; lateral regions flattened, axial regions inflated; fronto-orbital margin just under half maximum carapace width; orbits bilobed, directed forward and slightly upward; epigastric regions large, with two swellings; mesogastric region with two large nodes posteriorly, protogastric regions small, highly inflated; hepatic region flattened; branchial regions not well-differentiated.

Material examined.—*Sharnia burnhamensis*, holotype, (BMNH) IC.454.

Occurrence.—Ypresian (early Eocene) of U.K.

Discussion.—The holotype and sole specimen of *Sharnia burnhamensis* (Fig. 9) is incomplete, with all of its margins broken. The carapace ornamentation, the development of the axial regions, and the initially concave forward and then convex forward path of the cervical groove are suggestive of *Xanthosia* and *Etyus*, thus, the placement in Etyidae. More complete material with sternal elements will be necessary to confirm the placement.

Family FELDMANNIIDAE new family

Type genus.—*Feldmannia* Guinot and Tavares, 2001, by designation herein.

Included genera.—*Bretonia* new genus; *Caloxanthus* A. Milne-Edwards, 1864; *Feldmannia* Guinot and Tavares, 2001.

Diagnosis.—Carapace wider than long, hexagonal to ovoid outline, fronto-orbital width 60–80% maximum width; carapace grooves and regions typically not visible on carapace surface and subtly expressed on molds of interior of carapace; anterolateral margins with small spines or nodes; posterior margin generally straight or weakly concave and smooth. Sternum strongly deflexed at about midpoint of sternite 4; sternites 1–3 relatively short, triangular; episternite 4 quadrate, widest part of sternum, separating pereiopods 1 and 2; sternites 4 and 5 fused; pleonal locking mechanism may be present on sternite 5 or episternite 5 and coxae of pereiopods 1 and 2; sutures 5/6, 6/7, and 7/8 complete, sternite 8 small, strongly deflexed; spermathecal openings in females appearing to be located at axial end of sternite 7 or as an enlargement of suture 7/8, ovate; male gonopores situated very close to axial edge of coxae 5. Coxae of pereiopods 2–5 closely spaced; coxae 4 and 5 aligned at an angle greater than 70° to plane of carapace; pereiopod 5 subdorsal; because of steep angle of sternites 5–8 with 1–4, coxae forming steep arc with dorsal carapace. Male and female pleons with all pleonites free, each extending to point of inflection of sternite 4; male pleon straight-sided; female pleon weakly convex, covering entire sternum.

Discussion.—Guinot and Tavares (2001) erected *Feldmannia* to accommodate a single species, *Xanthosia wintoni* Rathbun, 1935. They noted several features that characterized the genus and distinguished it from *Xanthosia* sensu stricto and *Etyus*. These included weak areolation on the carapace; ornamentation consisting of densely packed granules over all of the carapace except behind the front, which is smooth; ovoid orbits directed somewhat upward; a weak slope at the level of sternite 8; male somite 2 twice as long as somite 1; coxa of pereiopod 5 either not smaller than those of pereiopods 2–4 or only slightly reduced; and meri of pereiopods 1–4 long, smooth, and strong. These characteristics distinguish *Feldmannia* from *Xanthosia* sensu stricto and *Etyus.* Examination of well preserved sternal elements on *Feldmannia wintoni* and *Caloxanthus americanus* Rathbun, 1935, provide evidence that the differences between these two taxa and *Xanthosia* sensu stricto and *Etyus* are significant enough to warrant erection of a new family, Feldmanniidae.

The sterna of both *Feldmannia* and *Caloxanthus* are strongly deflexed and the point of inflection is at about the midpoint of sternite 4. Sternites 1–3 are not produced longitudinally, and the unit is generally triangular. Sternites 4 and 5 are fused, whereas there are complete sutures 5/6, 6/7, and 7/8. The episternal projection on sternite 4 is large, quadrate, and broadly separates the coxae of pereiopods 1 and 2, whereas the coxae of pereiopods 2–5 are set close to one another. The coxae of pereiopods 4 and 5 define a steep plane at over 70° to the plane of the carapace. By contrast, the sternum on *Xanthosia* spp. is less strongly deflexed, sternites 1–3 are fused and are produced longitudinally with sternite 3 being more quadrate, the only complete suture is that of 5/6, the episternal projection on sternite 4 does not significantly separate the coxae of pereiopods 1 and 2, and the coxae of pereiopods 4 and 5 define a plane of about 45° with the plane of the carapace. These differences are judged to be sufficient to warrant the new family.

Because sternal features are often not preserved or are not exposed, it is important to note that there are several differences exhibited on the dorsal carapace that also distinguish the Etyidae from the Feldmanniidae. The overall aspect of the carapace in the Etyidae is one of well-developed regions and often a rather rough surface ornamented by nodes and spines, whereas that of taxa within Feldmanniidae densely granular or pustulose while regions are not particularly well-developed. The cardiac region and epibranchial regions are the most readily discernable. The cervical groove on species within Etyidae is broadly sinuous with a concave forward element distally, a convex forward element posterior to the protogastric region, and a concave element mesially. The cervical groove is typically

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not discernable at all on the cuticular surface of species within Feldmanniidae. On internal molds of the carapace, the regions are more strongly expressed and the cervical groove is visible. The course of the cervical groove is not as sinuous; the concave forward element seen on etyids is not present. Etyids also exhibit a pattern of grooves in the branchial region that are not present on feldmanniids. The two accessory grooves, herein designated bg1 and bg2, extend posterolaterally from the cervical groove to the posterolateral margin resulting in the characteristic fan-shaped arrangement of the lateral carapace of species of Etyidae. Finally, the anterolateral margin of etyiids tends to be more complex with nodes and nodose processes, whereas that of Feldmanniidae tends to be nearly smooth or only finely spinose. Thus, there are sufficient characters of the dorsal carapace that track the pattern seen on the sternum to permit identification even in the absence of the sternum.

Genus Feldmannia Guinot and Tavares, 2001

Type and only species.—*Xanthosia wintoni* Rathbun, 1935, by original designation and monotypy.

Diagnosis.—Carapace wider than long, hexagonal outline, carapace surface densely and finely spinose, with carapace grooves and regions typically not visible on cuticular surface and subtly expressed on internal molds; anterolateral margins with small spines; posterior margin generally straight, smooth. Sternum strongly reflexed at about midpoint of sternite 4; sternites 1–4 weakly granular; sternites 1–3 relatively short, triangular; episternite 4 quadrate, widest part of sternum, separating pereiopods 1 and 2; sternites 4 and 5 fused, sternite 5 with abdominal holding mechanism; sutures 5/6 and 6/7 complete, 7/8 nearly complete. Spermathecal opening ovoid, at axial end of sternite 7. Coxae of pereiopods 2–5 closely spaced; coxae 4 and 5 aligned at an angle greater than 70° to plane of carapace; because of steep angle of sternites 5–8 with 1–4, coxae forming steep arc with dorsal carapace. Male and female pleons unfused, each extending to point of inflection of sternite 4; male pleon straight-sided; female pleon weakly convex, covering entire sternum.

Feldmannia wintoni (Rathbun, 1935)
Figure 10

Xanthosia wintoni Rathbun, 1935, p. 42, pl. 11, figs. 6–8; Schweitzer Hopkins et al., 1999, p. 80, figs. 3, 4.

Feldmannia wintoni (Rathbun, 1935); Guinot and Tavares, 2001, p. 521, figs. 1D, 7D, 9C; Schweitzer et al., 2010, p. 67.

Diagnosis.—Carapace wider than long, hexagonal outline, carapace surface densely and finely spinose, with carapace grooves and regions typically not visible on cuticular surface and subtly expressed on internal molds; anterolateral margins with small spines; posterior margin generally straight, smooth. Sternum strongly reflexed at about midpoint of sternite 4; sternites 1–4 weakly granular; sternites 1–3 relatively short, triangular; episternite 4 quadrate, widest part of sternum, separating pereiopods 1 and 2; sternites 4 and 5 fused, sternite 5 with abdominal holding mechanism; sutures 5/6 and 6/7 complete, 7/8 nearly complete. Spermathecal opening ovoid, at axial end of sternite 7. Coxae of pereiopods 2–5 closely spaced; coxae 4 and 5 aligned at an angle greater than 70° to plane of carapace; because of steep angle of sternites 5–8 with 1–4, coxae forming steep arc with dorsal carapace. Male and female pleons unfused, each extending to point of inflection of sternite 4; male pleon straight-sided; female pleon weakly convex, covering entire sternum.

Description.—Small, hexagonal carapace, length 50–58% maximum width; weakly vaulted transversely, moderately vaulted longitudinally; regions poorly defined; ornamented with fine spines increasing in size anteriorly.

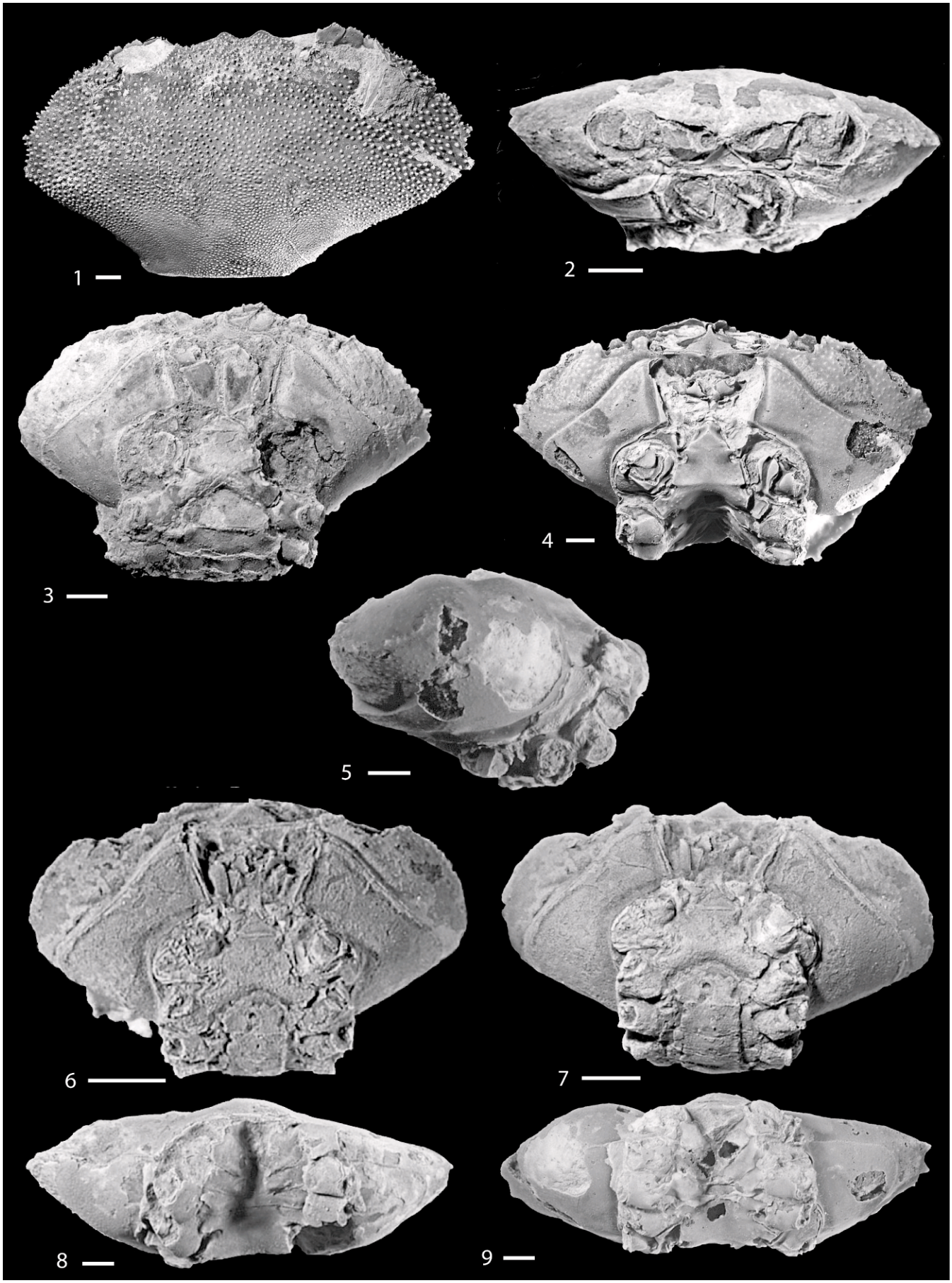
Front 29–35% maximum width measured posterior to midlength, axially sulcate, flanked by two broadly triangular projections; frontal margin finely beaded; frontal region set slightly below epigastric regions bounded by transverse, nodose ridge. Orbits ovoid, wider than high, bearing two closed supraorbital and two suborbital fissures that appear broadly open on internal mold of carapace; rim beaded; fronto-orbital width 56–62% maximum width. Anterolateral margin convex, bearing four or five small spines interspersed by fine spines. Posterolateral margin nearly straight, smooth, curving posteriorly at intersection with straight to weakly concave posterior margin which is 39–42% maximum width.

Carapace regions not readily discernable on carapace surface but relatively more distinct on internal mold of carapace. On cuticle exterior, small, circular epigastric regions are prominent, axial regions extending posteriorly from gastric pits smoothly elevated above branchial regions. On internal mold of cuticle, regions defined as subtle swellings; mesogastric region only slightly elevated, bearing longitudinal axial crest; metagastric/urogastric regions not differentiated; cardiac region pentagonal, with three distinct nodes, posteriormost axial; intestinal region short, indistinct; protogastric regions broadly swollen, with central elevation; hepatic region smooth, depressed. Cervical groove concave axially, convex posterior to hepatic region, intercepting lateral margin anterior to anterolateral spine; epibranchial region transversely elongate, weakly elevated, nodose; remainder of branchial area depressed, smooth.

Sternum narrow, strongly deflexed longitudinally. Sternites 1–3 and anterior part of 4 slightly inclined anterodorsally, flat. Posterior part of sternite 4 and sternites 5–8 strongly sloping posterodorsally and transversely concave. Sternites 1–2 a small triangular element with transverse ridge (Fig. 10.4); sternite 3 broadly triangular, with subtle suture between 3 and 4 visible on mold of sternum but appearing as incomplete on cuticle surface. Sternite 4 widening posteriorly to maximum sternal width at prominent, bluntly terminated episternal projections separating pereiopod 1 from pereiopod 2. Sternites 4 and 5 fused. Sternites 6–8 with deep axial cleft (Fig. 10.9), well developed sutures 5/6, 6/7, and 7/8; suture 7/8 complete except for extremely narrow axial fusion in axial cleft. Each sternite from 5–8 progressively narrowing and more directed posterolaterally. Male gonopores near postero-axial corner of coxa of pereiopod 5, ovoid (Fig. 2.5); female gonopore in similar position of coxa of pereiopod 3. Spermathecal opening situated on axial tip of sternite 7 (Fig. 2.1).

Male pleon unfused, narrow, straight-sided, with rounded triangular telson reaching sternite 4 at level of inflection of sternum (Fig. 10.6). Pleonites slightly elevated axially, rounded laterally, otherwise smooth. Female pleon with convex margins, extending to coxae of pereiopods (Fig. 10.3), covering entire surface of sternites 5–8, terminating at level of deflection of sternum. Axial and, to lesser extent, lateral parts of pleonites elevated. Male and female pleonites 1, 2, and part of 3 visible dorsally (Fig. 10.3, 10.6, 10.7).

Antennal fossae nearly as large as orbits (Fig. 10.2); basal antennal article large, inflated, with longitudinally elongate slit. Eyestalks short, stout, granular. Optical surface convex, small. Mandibles relatively large, strong, with fine serrations at least on right mandible. Maxilliped 3 operculiform, filling buccal frame which broadens anteriorly; ischium set in plane of carapace surface, merus inclined anterodorsally. Coxa of pereiopod



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1 larger than those of pereiopods 2–5, and separated from them by episternal projection of sternite 4 (Fig. 10.4). Coxae of pereiopods 2–5 set close together (Fig. 10.7). Coxae of pereiopods 2 and 3 larger than pereiopods 4 and 5. Pereiopods 2–5 form steepening posteriorly arc relative to carapace surface so that pereiopods 4 and 5 are almost perpendicular to carapace surface (Fig. 10.5).

Material examined.—*Feldmannia wintoni*, USNM 543681, 543682, 543684–89.

Occurrence.—The type series was collected from the upper Albian Denton Clay in Grayson County, Texas, and from the upper Albian Pawpaw Formation in Tarrant County, Texas. For specific details see Rathbun (1935, p. 42, 136). Material in the present study was collected from seven localities within the Pawpaw Formation in Ft. Worth, Tarrant County, Texas (Table 1).

CALOXANTHUS A. Milne-Edwards, 1864 (=CARPILIOPSIS von Fischer-Benzon, 1866; CRETICARCINUS Withers, 1928)

Type species.—*Caloxanthus formosus* A. Milne-Edwards, 1864, by monotypy.

Included species.—*Caloxanthus americanus* Rathbun, 1935; *C. kuypersi* Fraaye, 1996; *C. formosus* A. Milne-Edwards, 1864; *C. ornatus* (von Fischer-Benzon, 1866), as *Carpiliopsis*; *C. purleyensis* (Withers, 1928), as *Cretacarcinus*; *C. simplex* (Secretan, 1964), as *Carpiliopsis*; *C. wrighti* Collins and Breton, 2011.

Diagnosis.—Carapace wider than long, ovoid, carapace surface densely and coarsely to finely pustulose, with carapace grooves and regions typically not visible on cuticular surface, subtly expressed on internal molds of carapace; anterolateral margins with small nodes; posterior margin generally straight, smooth. Sternum strongly deflexed at about midpoint of sternite 4; sternites 1–3 relatively short, triangular; sternites 1–4 coarsely granular; episternite 4 quadrate, widest part of sternum, separating pereiopods 1 and 2; sternites 4 and 5 fused; sutures 5/6, 6/7 complete, and 7/8 appearing complete but obscured axially; spermatheca in females long, ovate, situated on sternal suture 7/8. Coxae of pereiopods 2–5 closely spaced; coxae 4 and 5 aligned at an angle greater than 70° to plane of carapace. Pereiopod 5 more slender than pereiopods 2–4, carried dorsally over carapace. Male and female pleons unfused, each extending to point of inflection of sternite 4; male pleon straight-sided; female pleon weakly convex, covering entire sternum.

Discussion.—The concept of *Caloxanthus* as originally conceived by A. Milne-Edwards (1864) and as subsequently applied has been based upon characters of the dorsal carapace. A. Milne-Edwards' illustrations (1863, pl. 9, fig. 1, 1a–1d) conform closely to the diagnosis of the Feldmanniidae herein. The carapace is wider than long, has orbits that are circular and directed antero-dorsally, exhibits only subtle definition of regions with the cardiac region being most prominent, and lacks definition of the cervical groove. The coarse granular or pustulose ornamentation and finely spinose anterolateral margin and smooth posterolateral margin are hallmarks of the genus.

Examination of descriptions and illustrations of taxa subsequently referred to the genus confirm that the concept of the genus has been expanded. Many of the specimens upon which species have been named are quite fragmentary and their placement is dubious.

Caloxanthus americanus closely conforms to the original concept of the genus and, as will be described below, provides valuable information regarding the sternal, pleonal, and appendage morphology lacking in the original and other subsequently named species. It is noteworthy that the specimen illustrated as *Caloxanthus americanus* by Wright and Collins (1972, pl. 21, fig. 7) exhibits margins that do not resemble those of the American specimens, although the specimen illustrated in their plate 22, figures 1a and b, closely resembles *C. americanus*. *Caloxanthus kuypersi* is based upon a single fragmentary specimen that bears pustulose ornamentation, has weak expression of regions, and no indication of a cervical groove; however, the front is projected well beyond the orbits which are directed anterolaterally, as is typical of the type species. Until better and more complete material is found, the specimen can be provisionally included in the genus. *Caloxanthus ornatus* as illustrated (von Fischer Benzon, 1866, pl. 2, figs. 1–3) and described (1866, p. 28), formed the basis for creation of a new genus, *Carpiliopsis*. That genus was subsequently considered synonymous with *Caloxanthus* (Glaessner, 1969, p. R517). As illustrated by von Fischer-Benzon, the specimen conforms to the diagnosis of *Caloxanthus* in the shape of the front, the shape and orientation of the orbits, and the general size and outline. The specimen illustrated seems to be decorticated, and regional development is more prominent than would be anticipated on the surface of the cuticle. However, details of comparison must await examination of the type material. A transverse feature representing the cervical groove is consistent with that in the Feldmanniidae, but a second transverse structure posterior to it is problematic, and interpretation of it cannot be done accurately from the illustration. *Caloxanthus purleyensis* (Withers, 1928) was originally placed in a new genus, *Creticarcinus* Withers, 1928; subsequently this was considered synonymous with *Caloxanthus* (Glaessner, 1969, p. R517). The sole specimen closely resembles *C. formosus* in most regards. However, the lateral margins are somewhat more rounded so that there is no inflection between anterolateral and posterolateral margins, and the cervical groove is moderately well-defined axially and becomes obscure laterally. Secretan (1964) originally assigned *Caloxanthus simplex* to *Carpiliopsis*. Based upon her description, the species seems to be conformable to the concept of *Caloxanthus* except in terms of the surface ornamentation. Secretan (1964, p. 184) noted that the carapace was smooth. Examination of her illustrations (1964, pl. 19, figs. 8–10) are difficult to interpret so that it is not possible to discern whether or not the cuticle is intact. If cuticle is not present, the absence of a pustulose surface would be understandable. Recently, Collins and Breton (2011) illustrated newly recognized specimens of *C. formosus* from the Cenomanian of France, and they recognized a new species, *C. wrighti*, from Santonian rocks in France. The specimen upon which the species was named is a well preserved dorsal carapace originally judged to

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FIGURE *10*—Feldmanniidae, *Feldmannia wintoni* (Rathbun, 1935). *1*, USNM 543684, dorsal carapace showing well preserved anterolateral margin and ornamentation; *2*, USNM 543685, anterior view; *3*, USNM 543686, female pleon; *4*, *5*, *9*, USNM 543687: *4*, male sternum, showing marked deflexion of sternum at position of sternites 4/5; *5*, lateral view showing posteriorly positioned pleon and vertical position of pereiopods 3–5; *9*, posterior view of male sternum (9); *6*, *7*, USNM 543688: *6*, male third maxillipeds; *7*, pleon and sternum; *8*, USNM 543689, deep sterno-abdominal cavity. Scale bars=1 mm.

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be a subset of *C. formosus*, although they did not formally name it a subspecies. *Caloxanthus wrighti* exhibits a more ovoid outline than typical *Caloxanthus* and it has a convex posterolateral margin rather than being straight. Also, the regions are rather more prominent than on the type species or on *C. americanus*; however, the regions are not as well defined as in *C. purleyensis*. In other regards *C. wrighti* conforms well to the concept of *Caloxanthus.*

Caloxanthus americanus Rathbun, 1935
Figure 11

Caloxanthus americanus Rathbun, 1935, p. 56, pl. 11, figs. 12–19. Schweitzer et al., 2010, p. 67.

Diagnosis.—Carapace ovoid to hexagonal, wider than long, ornamented with closely spaced granules overall; orbits ovoid, wider than high, entire, directed upward and moderately anterolaterally; rim elevated; anterolateral margin convex, bearing four or five small granules; carapace regions undefined; chelipeds stout, with black fingers.

Description.—Carapace ovoid to hexagonal, length 66–75% maximum width measured at about midlength; weakly vaulted transversely, moderately vaulted longitudinally; regions poorly defined; ornamented by closely spaced, coarse pustules on cuticle surface and expressed as granules on internal mold of carapace.

Front about 32% maximum width, axially deeply sulcate, projected slightly in advance of orbits. Orbits ovoid, wider than high, entire, directed upward and moderately anterolaterally; rim elevated, granular; fronto-orbital margin 73–79% maximum width. Anterolateral margin convex, bearing four or five small granules. Posterolateral margin convex, weakly granular, with short concave curve at intersection with straight to weakly concave posterior margin, about 43% maximum width.

Carapace regions obscure on carapace surface and weakly expressed on internal mold of carapace. On internal mold, regions reflected as subtle swellings; epigastric regions elevated as small nodes; pyriform mesogastric region set below broadly swollen protogastric regions ornamented with small central node; hepatic regions indistinct; mesogastric region transversely broad, longitudinally short, bearing axial node; urogastric region small, depressed; cardiac region prominent, pentagonal, with three distinct nodes, posteriormost axial; intestinal region short, depressed. Cervical groove indistinct. Branchial regions generally undifferentiated, more swollen anteriorly, less so posteriorly.

Sternum narrow, strongly deflexed longitudinally (Fig. 11.7). Sternites 1–3 and anterior part of 4 slightly inclined anterodorsally (Fig. 11.7). Posterior part of sternites 4 and 5–8 steeply sloping posterodorsally and transversely concave. Sternites 1–3 incomplete, appearing to be triangular. Sternite 4 broadening posteriorly to maximum sternal width, with quadrate episternal projections separating coxae of pereiopod 1 from pereiopod 2. Two nodes situated on sternite 4 at point of inflection of surface. Surface of sternites 1–4 coarsely granular. Sternites 4 and 5 fused. Sternites 6–8 concave, well-developed, entire sutures between sternites 5/6 and 6/7; 7/8 obscured. Sternites 5–8 narrowing progressively posteriorly, strongly directed posterodorsally. Surface of sternites 5–8 smooth. Spermathecal openings elongate, ovate, situated on sternal suture 7/8 (Fig. 2.2). Binodal locking device situated at lateral margin of episternal projection 5.

Male pleon unfused, narrow, straight sided, pleonites 2–6 equal in length, somite 1 shorter, narrower than other somites; telson with rounded tip; surface of pleon granular (Fig. 11.2). Male pleon extending to point of inflection of sternite 4. Female pleon with convex margins, sternites about equal in length; telson longer than that of male, tapering distally; surface of female pleon granular.

Eyestalks short, smooth proximally, granular near small, convex optical surface. Maxilliped 3 operculiform, apparently filling quadrate buccal cavity which broadens anteriorly; ischium set in plane of carapace surface, merus inclined anterodorsally.

Coxa of pereiopod 1 larger than those of pereiopods 2–5 and separated from them by episternal projection of sternite 4 (Fig. 11.2). Coxae of pereiopods 2–5 set close together; that of pereiopod 5 smaller than those of pereiopods 2–4. Pereiopods 2–5 form steepening posteriorly arc relative to carapace surface so that pereiopods 4 and 5 are almost perpendicular to carapace surface.

Ischium, merus, carpus, and manus of cheliped stout, inflated, coarsely granular. Proximal surfaces of fingers granular, becoming smooth with longitudinal grooves on inner, outer, and upper surface of dactyl and on inner and outer surfaces of fixed finger (Fig. 11.4–11.6). Occlusal surface with strong, triangular teeth occluding tightly by being set at alternating distances from hand. Remainder of pereiopods with long, slender, flattened meri, bearing two rows of fine granules on lower surface, otherwise generally smooth. P5 carried dorsally over the carapace (Fig. 11.1, 11.2).

Material examined.—Nineteen specimens of *Caloxanthus americanus* from four localities in the Pawpaw Formation in Ft. Worth, Tarrant County, Texas were studied. Of these, USNM 543694–96, 543699–700 are illustrated. Details of the collecting sites are given in Table 1.

Discussion.—The specimens from the Weno and Pawpaw formations provide information about the sternal characteristics, pleonal morphology, and nature of appendages that have not been described previously. These characteristics are important in confirming placement within the Feldmanniidae.

It is interesting to note the difference in preservational style of specimens of *Caloxanthus americanus* and *Feldmannia wintoni*. The former is commonly preserved with the legs attached, whereas that is rarely the case with specimens of *Feldmannia.* On the other hand, the preservation of the carapace on specimens of *F. wintoni* tends to be good so that the outline and convexity of the material can be accurately determined. The outline of specimens of *C. americanus* is often poorly preserved, and some of the specimens are crushed or distorted so that the overall form must be interpreted from examination of several specimens.

Genus Bretonia new genus

Type species.—*Xanthosia danielae* Collins and Breton, 2009, by designation herein.

Etymology.—The generic name honors Gérard Breton, Université de Rennes, France, for his important contributions to the understanding of decapods from France. The gender is feminine.

Diagnosis.—Carapace wider than long; frontal margin about 34% maximum carapace width measured posterior to midlength; fronto-orbital margin about 58% maximum width; anterolateral margins convex, bearing five short projections; posterolateral margin straight to weakly concave; posterior margin about 37% maximum width, concave. Surface of carapace generally smooth with cardiac region slightly elevated above weakly vaulted overall surface; carapace grooves indistinct.

Discussion.—Collins and Breton (2009) named *Xanthosia danielae* for material collected from the Cenomanian of Le Mans, France. The specimens consist of internal molds of the carapace and broken parts of anterior sternites, as well as the terminal somite and telson of the pleon. Unfortunately, the sternum is not well enough preserved to further confirm placement within the

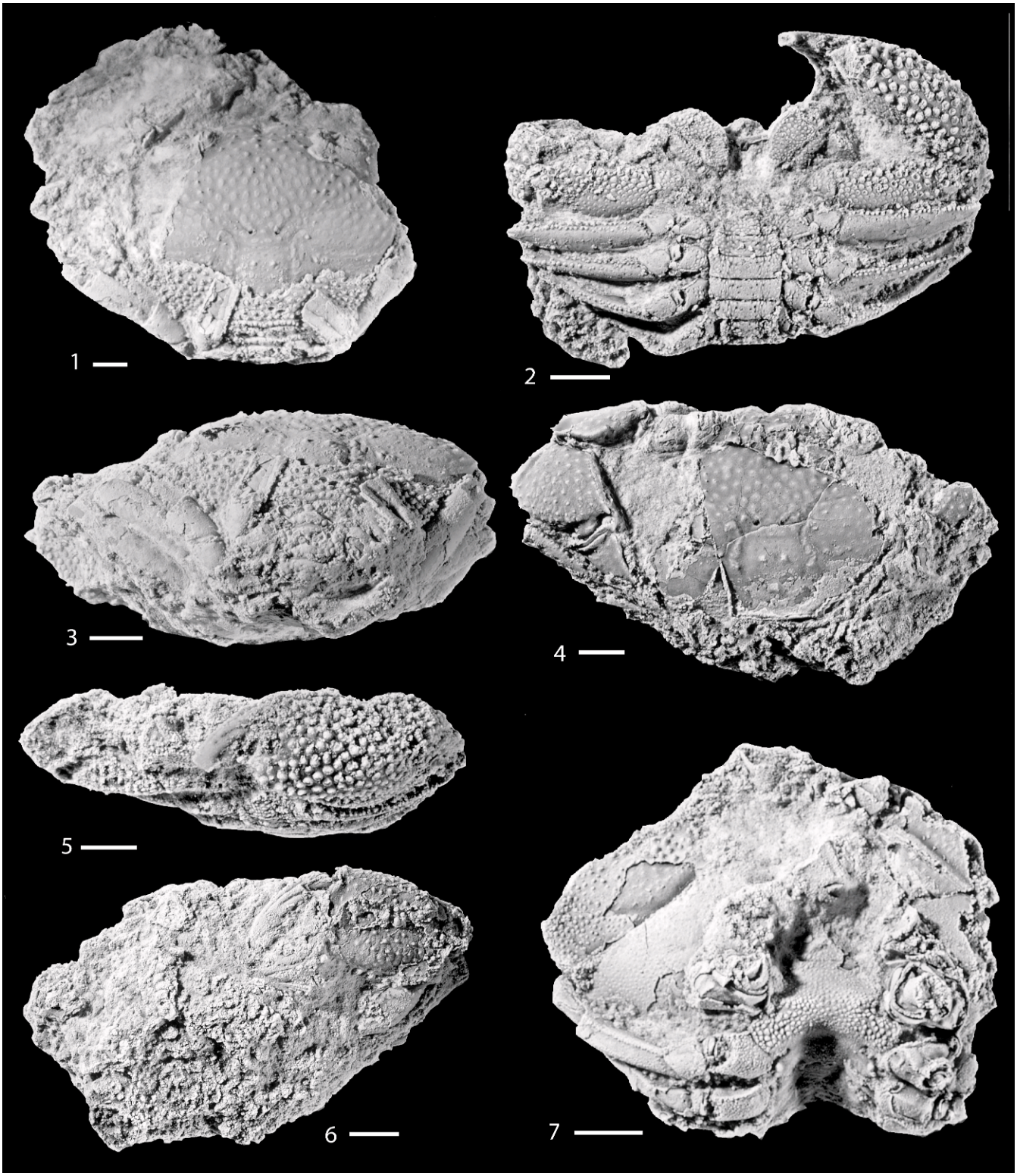

FIGURE *11*—Feldmanniidae, *Caloxanthus americanus* Rathbun, 1935. *1*, *3*, USNM 543694: *1*, dorsal surface showing dorsally carried fifth pereiopod; *3*, posterior view showing dorsally carried fifth pereiopod; *2*, USNM 543695, male ventral surface; *4*, *5*, *6*, USNM 543696: *4*, dorsal carapace; *5*, left cheliped; *6*, ventral surface and left cheliped; *7*, USNM 543700, male sternum. Scale bars=1 mm.

Feldmanniidae; however, the triangular nature of sternites 1–3 is similar to that seen in *Feldmannia* and *Caloxanthus*.

Based upon the morphology of the dorsal carapace, it is not possible to retain the species in *Xanthosia*. The smooth, almost featureless nature of the carapace resembles *Feldmannia*. *Xanthosia* sensu stricto has a well defined, sinuous cervical groove with a concave forward configuration posterior to the hepatic region. The branchial regions in species of *Xanthosia* bear two accessory grooves extending posterolaterally from the cervical groove. The anterolateral margin tends to be projected into spiny lobes.

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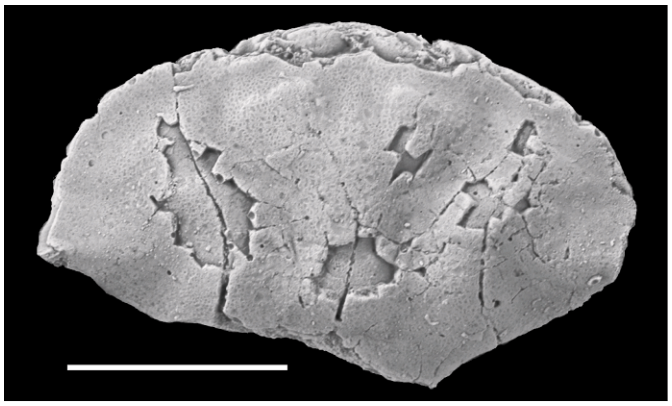

FIGURE *12*—Aethridae, *Eriosachila*? *robertsi* (Secretan, 1982), MNHN R03979, holotype. Scale bar=1 cm.

Bretonia danielae cannot be placed in *Feldmannia* or in *Caloxanthus* because *B. danielae* has orbits that are only slightly directed upward, exhibits a more angular anterolateral corner and a more concave posterolateral margin, and has a much smoother overall appearance of the mold of the interior of the carapace. Moldic preservation on species of both *Caloxanthus* and *Feldmannia* reveals much more detail of the region and groove patterns than does the surface of the cuticle. That is not the case with *Bretonia.* Therefore, considering the diagnoses of *Xanthosia* and comparison of *G. danielae* to the genera within Feldmanniidae, it is necessary to erect a new genus, *Bretonia*, to accommodate *Bretonia danielae* (Collins and Breton, 2009).

Section EUBRACHYURA de Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Superfamily CALAPPOIDEA De Haan, 1833
Family AETHRIDAE Dana, 1851
Genus ERIOSACHILA Blow and Manning, 1996

Type species.—*Eriosachila petiti* Blow and Manning, 1996, by original designation.

Diagnosis.—Carapace hexagonal to octagonal, wider than long, widest at second or third anterolateral spine; regions developed as broad or discrete inflated areas, axial region and protogastric regions outlined by moderate groove; front weakly projecting beyond orbits, axially notched; orbits small, subcircular; anterolateral margins convex, with three or four blunt spines; posterolateral margins concave, with two or three spines; posterior margin narrow (after Schweitzer and Feldmann, 2000).

GENUS ERIOSACHILA? ROBERTSI (Secretan, 1982)
Figure 12

Xanthosia elegans SECRETAN, 1964, p. 178, pl. 20, figs. 4–6.
Xanthosia robertsi SECRETAN 1982, p. 928 (replacement name); GUINOT AND TAVARES, 2001, p. 517.
"*Xanthosia robertsi*." SCHWEITZER HOPKINS et al., 1999, p. 80.
"*Xanthosia*" sensu lato *X. robertsi* SECRETAN, 1982. SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace wider than long; anterolateral margins crispate, appearing to have been tightly convex, last anterolateral spine extending onto carapace as broad ridge; posterolateral margin nearly straight; well developed groove outlining protogastric region, then arcing around metagastric, urogastric, and cardiac regions; hepatic and branchial regions confluent, broad swelling extending from hepatic region onto branchial region.

Remainder of carapace and appendages unknown.

Type.—MNHN R03979, holotype.

Occurrence.—Early Campanian (Late Cretaceous) of Madagascar.

Discussion.—*Xanthosia robertsi* lacks the cervical groove that is present in all member of Etyidae. In addition, it lacks the oblique branchial grooves and the oblique mesobranchial region seen in most Etyidae or Feldmanniidae. It has a well developed groove that outlines the protogastric regions and then arcs around the metagastric, urogastric, and cardiac regions, a feature not seen in any members of Etyidae or Feldmanniidae. This type of pattern, in which the axial regions are well-outlined, is commonly seen in Calappidae and Aethridae. The hepatic regions and branchial regions are confluent, and an arcuate swelling extends from the hepatic region to the branchial region, features not seen in any Etyidae. There is evidence of a lateral spine that extends onto the carapace as a broad ridge. Unfortunately, the front, orbits, and margins are broken in the holotype and sole specimen of *X. robertsi*, making it difficult to place this species within a genus or even a family.

We suggest that *Xanthosia robertsi* has most close affinities with Aethridae, based upon the ovate carapace, tightly convex anterolateral margins, and position of maximum width at about the midlength and not posteriorly as seen in many calappids. However, much more complete material will be necessary to assign it to a family and genus with confidence. For now, we place it questionably within the Aethridae. We have elected to place it within the genus *Eriosachila*, based upon the presence of the groove outlining the protogastric and axial regions. This is not a perfect fit, as members of *Eriosachila* have better developed ornamentation, as distinct spherical swellings on the carapace, and species of *Eriosachila* are narrower than *X. robertsi*. However, the type and only specimen of *X. robertsti* is poorly preserved, with little of its margins intact, and so we believe it imprudent to erect a new genus on such incomplete material. Referral of *X. robertsi* to *Eriosachila* does extend the range of the genus from Eocene to Late Cretaceous and from the Americas and Egypt to Madagascar. It does not extend the geologic range of the family, which is known from Cretaceous occurrences of *Prehepatus* Rathbun, 1935 (summary in Schweitzer et al., 2006), for which unfortunately, a carapace has never been reported. In any event, *X. robertsi* is neither a member of *Xanthosia* nor Etyidae and must be removed from the genus and the family. *Eriosachila* and Aethridae seem to be the best fit, causing the least disruption, at this time.

Superfamily PORTUNOIDEA Rafinesque, 1815
Family MACROPIPIDAE Stephenson and Campbell, 1960

Included genera.—See Schweitzer et al. (2010).

Diagnosis.—Carapace moderately broad, length 65–80% maximum carapace width, widest between 50–60% the distance posteriorly, usually 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% maximum carapace width, rarely approaching 90% (*Coenophthalmus* and some *Proterocarcinus*); front spined, number and size of spines variable, usually with an axial notch but sometimes with an axial spine (*Macropipus*), front ranging from 20–40% maximum carapace width but rarely reaching 60% (*Coenophthalmus*); 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 pereiopods; male abdominal pleonites 3–5 fused and usually with clear evidence of sutures or indentations in the margins marking the position of pleonites or all male pleonites

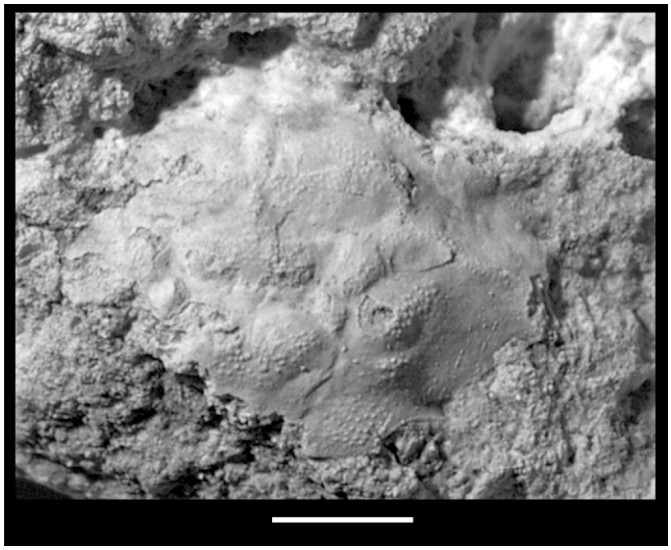

FIGURE 13—Macropipidae, *Maeandricampus americanus* (Rathbun, 1930), USNM 371098, holotype. Scale bar=1 mm.

free, somite three and sometimes others with transverse keels, somite three generally markedly wider than other pleonites, 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 with occasional exception of 6/7 and 7/8 (*Nectocarcinus*); portunid lobe usually present; basal antennal article fixed or free, usually lacking laterodistal spines; chelae usually keeled; some pereiopods as long as chelipeds; dactylus of fifth pereiopod oblanceolate or obovate, rarely ovate and paddle-like in traditional sense (*Parathranites*) (Karasawa et al., 2008, p. 100)

Genus MAEANDRICAMPUS Schweitzer and Feldmann, 2002

Type species.—*Portunites triangulum* Rathbun, 1926, by original designation.

Other species.—*Maeandricampus americanus* (Rathbun, 1930); *M. granuliferus* (Glaessner, 1960).

Diagnosis.—Carapace wider than long, length about 65% 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 refined, 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.

MAEANDRICAMPUS AMERICANUS (Rathbun, 1930)
new combination
Figure 13

Xanthosia americana RATHBUN, 1930, p. 3, pl. 6, fig. 1.
"*Xanthosia*" sensu lato *X. americana* RATHBUN, 1930; SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace tiny, appearing to be wider than long; protogastric regions with transverse ridges; orbits wide, occupying most of carapace width, with two fissures; epibranchial region with arcuate ridge terminating in stout anterolateral spine; branchial regions with three swellings arranged in triangular pattern; cardiac region with two large swellings.

Material examined.—*Xanthosia americana*, USNM 371098, holotype.

Remarks.—Rathbun (1930) described a new species of *Xanthosia* from the Oligocene of Baja California Sur. The specimen is absolutely tiny (about 0.5 cm) in size, and it is so poorly preserved and blends in so well with the surrounding rock that two of us (CES and RMF) initially thought that the specimen had been lost. Reexamination of the holotype specimen of *Xanthosia americana* at the USNM confirms that the specimen is extant and cannot be referred to *Xanthosia*. The broad orbits with two fissures; arcuate epibranchial region that terminates in a stout lateral spine; three epibranchial swellings arranged in a triangular pattern; and two clear cardiac swellings indicate placement in Macropipidae, specifically *Maeandricampus*. Placement of *Xanthosia americana* in this genus does not extend the geologic range, as it was already known from the Eocene of New Zealand and the Oligocene–Miocene of the Pacific coast of Washington, U.S.A. (Schweitzer and Feldmann, 2002). The geographic range would be extended southward into Baja California Sur by the placement, but this type of range, all along the Pacific coast during the Eocene through the Miocene, is not uncommon for decapods (Schweitzer, 2001; Schweitzer et al., 2003). Thus, we place Rathbun's species within *Maeandricampus*, resulting in *M. americanus* new combination.

Genus FAKSECARCINUS new genus

Type species.—*Xanthosia gracilis* Jakobsen and Collins, 1997, by original designation.

Diagnosis.—Carapace ovate, wider than long, length about 60% 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% 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.

Etymology.—The genus is derived from the Fakse Quarry, Denmark, where the specimens of the type species were collected, and the Greek word karkinos, meaning crab, a common stem in the Infraorder Brachyura. The gender is masculine.

Material examined.—MGUH 24367.

Discussion.—*Xanthosia gracilis* cannot be referred to *Xanthosia* or the Etyidae based upon its lack of a well-developed cervical groove and an oblique mesobranchial region, broad orbits and front, front that protrudes well beyond the orbits, deep orbits that are oriented anterolaterally, and poorly defined regions. *Faksecarcinus* lacks bg1, bg2, and the oblique mesobranchial region typical of etyids and has well defined, deep orbits and a front not characteristic of Etyidae. Thus, we refer the species to a new genus, *Faksecarcinus*, herein.

The position of *Faksecarcinus* at the family level is somewhat problematic, especially because there are no appendages, sternum, or pleon preserved. The best placement for it seems to be with the Macropipidae, at least at this time. Macropipidae can accommodate brachyurans that are wider than long, with a sulcate front, broad orbits, a frontal margin of about half the maximum carapace width, a fronto-orbital width that may be over 60% the maximum carapace width, and an anterolateral margin with three to five spines with the last spine markedly

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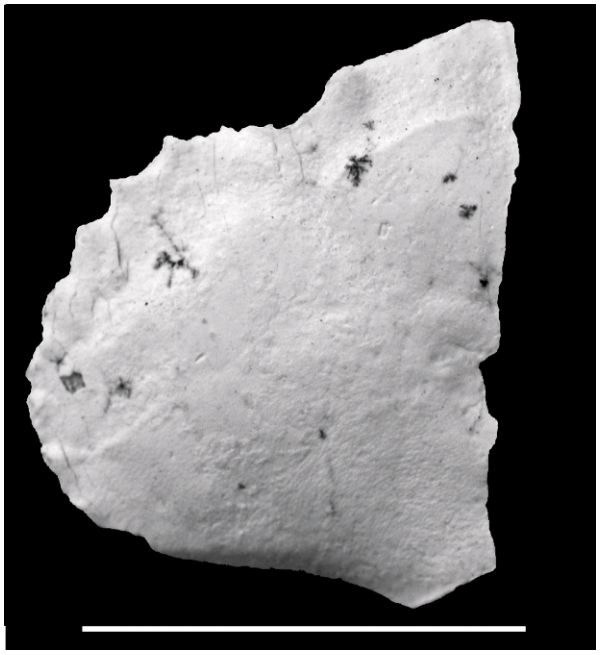

FIGURE *14*—Brachyura *incertae sedis*, *Xanthosioides delicata* (Fraaye, 1996), MAB k.1960, holotype. Scale bar=1 cm.

longest. The fit within the Macropipidae is not perfect, as *Faksecarcinus* seems to lack an arcuate epibranchial region and longitudinal ridges on the metabranchial regions; however, we note that the specimens of *Faksecarcinus gracilis* lack cuticle, so it is difficult to determine what the actual ornamentation of the cuticle would have been. *Faksecarcinus* ranges from the Albian–Cenomanian of Spain (unpublished records of AK) to the Danian of Denmark; this does not extend the geologic range of the family which was already known from the early Cretaceous of North America. The family was well-established throughout Europe by the Eocene.

FAKSECARCINUS GRACILIS (Jakobsen and Collins, 1997)

Xanthosia gracilis JAKOBSEN AND COLLINS, 1997, p. 95, pl. 2, figs. 1, 2.

"*Xanthosia*" sensu lato *X. gracilis* JAKOBSEN AND COLLINS, 1997; SCHWEITZER et al., 2010, p. 131.

Diagnosis.—Carapace ovate, wider than long, length about 60% 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% 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.

Description.—Carapace ovate, wider than long, length about 62% maximum width, widest about two-thirds the distance posteriorly on carapace at position of last anterolateral spine.

Front broadly bilobed, deeply axially sulcate, broadly convex on either side of sulcus, front wide, about 40% maximum carapace width. Orbits deep laterally, directed obliquely anterolaterally, weakly rimmed, with two open fissures, outer fissure widest and deepest, fronto-orbital width 70% maximum carapace width. Anterolateral margins with 4 spines including outer-orbital spine, spines increasing in size posteriorly, last spine long, attenuated, margin tightly convex; posterolateral margin convex; posterior margin narrow, concave.

Carapace regions only known from mold of interior; epigastric regions small, equant; mesogastric region triangular, with two small swellings posteriorly and muscle scars along posterior margin; metagastric region ornamented with muscle scars; urogastric region narrow, with concave lateral margins; cardiac region triangular, with three swellings, one at each apex. Protogastric region broad, weakly inflated; hepatic region poorly differentiated from branchial regions, the two are differentiated by a sprinkling of nodes and muscle scars.

Occurrence.—Danian of Denmark (Jakobsen and Collins, 1997) and Albian–Cenomanian of Spain (AK).

BRACHYURA incertae sedis
XANTHOSIOIDES Collins and Breton, 2009

Type species.—*Xanthosia delicata* Fraaye, 1996, by original designation.

Diagnosis.—Carapace wider than long, length about 60% maximum width, widest about half the distance posteriorly on carapace; front possibly axially sulcate, about 30% maximum carapace width; orbits directed forward, with two closely spaced, long, closed fissures; anterolateral margins tightly convex, crispate, spinose; posterolateral margins broadly concave; posterior margin concave; protogastric region with narrow ridge parallel to anterior margin; branchiocardiac groove appearing to be developed as arcuate depressions along urogastric region.

Material examined.—Holotype, MAB k1960.

Occurrence.—Maastrichtian of The Netherlands.

Discussion.—Fraaye (1996) erected a new species for incomplete material, which Collins and Breton (2009) then placed within a new genus. The incomplete nature of the material makes it difficult to place within a family. Only about half of the carapace is preserved (Fig. 14), and the nature of the breakage makes it nearly impossible to determine how to orient the remaining half. The reconstruction of Fraaye (1996, pl. 1, fig. 1) shows, at the anterior edge, what appears to be an axial groove just to the left of the break. However, in the mirror image that was made, the axial groove has been "mirrored in" so that there are two axial grooves; thus, we think that this reconstruction cannot be correct if in fact this groove is an axial groove. An additional problem is in knowing at what angle to place the fan-shaped anterolateral margins. Brachyurans differ in the convexity of the anterolateral margin, ranging from tightly convex and with the majority of the spines facing more anteriorly to tightly convex and with the majority of the spines directed more laterally as reconstructed by Fraaye (1996). Either could be correct given the material at hand.

All of this shows that this specimen could be reconstructed in several ways. The damaged nature of the margins, which nevertheless were surely spinose and crispate, suggests that it may have been an aethrid or possibly a member of the Cancridae, Xanthoidea, or Eriphioidea. However, until more complete material can be recovered, we elect to leave this genus unplaced at the family level.

XANTHOSIA ZOQUIAPENSIS Fraaije, Vega, van Bakel, and Garibay-Romero, 2006

Discussion.—*Xanthosia zoquiapensis* was reported from Campanian (Late Cretaceous) rocks of Guerrero, Mexico. It is based upon fragmental material that is not referable to *Xanthosia*, and does not appear to be referable to the Etyidae. The front is broadly quadrilobed, the fronto-orbital width

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TABLE 2—Species at one time referred to *Xanthosia* and their placement according to the classification presented in this paper.

Species (original generic placement listed)	Current placement	Family	Range
Xanthosia gibbosa (type)	*Xanthosia*	Etyidae	Cenomanian, U.K.
Xanthosia elegans	*Xanthosia*	Etyidae	Campanian, New Jersey, U.S.A.
Xantho fischeri	*Xanthosia*	Etyidae	Cenomanian, France
Xanthosia semiornata	*Xanthosia*	Etyidae	Maastrichtian, The Netherlands
Xanthosia buteonis	*Etyus*	Etyidae	Albian, U.K.
Reussia granulosa	*Etyus*	Etyidae	Albian, U.K.
Xanthosia jacksoni	*Etyus*	Etyidae	Aptian, U.K.
Xanthosia sakoi	*Etyus*	Etyidae	Barremian, Japan
Etyus similis	*Etyus*	Etyidae	Albian, U.K.
Xanthosia fossa	*Etyxanthosia*	Etyidae	Albian–Cenomanian Spain; Cenomanian, U.K.
Xanthosia aspera	*Steorrosia*	Etyidae	Albian–Cenomanian, Texas, U.S.A.
Xanthosia pawpawensis	*Steorrosia*	Etyidae	Albian–Cenomanian, Texas, U.S.A.
Xanthosia reidi	*Steorrosia*	Etyidae	Albian–Cenomanian, Texas, U.S.A.
Xanthosia arcuata	*Secretanella*	Etyidae	Cenomanian, Madagascar
Podophthalmus buchii	*Secretanella*	Etyidae	Turonian, Czech Republic
Xanthosia occidentalis	*Secretanella*	Etyidae	Campanian, South Dakota, U.S.A.
Xanthosia socialis	*Secretanella*?	Etyidae	Campanian, Germany
Xanthosia spinosa	*Secretanella*	Etyidae	Campanian, Colorado, U.S.A.
Xanthosia wintoni	*Feldmannia*	Feldmanniidae	Albian–Cenomanian, Texas, U.S.A.
Xanthosia danielae	*Bretonia*	Feldmanniidae	Cenomanian, France
Xanthosia robertsi	*Eriosachila*?	Aethridae	Campanian, Madagascar
Xanthosia americana	*Maeandricampus*	Macropipidae	Oligocene, Baja California Sur, Mexico
Xanthosia gracilis	*Faksecarcinus*	Macropipidae?	Danian, Denmark
Xanthosia delicata	*Xanthosioides*	Brachyura incertae sedis	Maastrichtian, The Netherlands
Xanthosia zoquiapensis	Brachyura incertae sedis	Brachyura incertae sedis	Campanian, Guerrero, Mexico

appears to occupy about 74% the maximum carapace width, much higher than taxa within Etyidae; the outer-orbital spine is stout and forward-directed; the anterolateral margins are straight and composed of closely spaced, blunt spines; and the epibranchial region is arcuate, extending from the last anterolateral spine to the axial regions. None of these are features of *Xanthosia* or Etyioidae. In addition, examination of an illustration of the holotype specimen (Fraaije et al., 2006, fig. 3.3) indicates that it is has been sheared. The mesogastric region is assymetrical and the urogastric region appears to be shifted laterally with respect to the mesogastric region. Also, both illustrated specimens are incomplete. We suggest that more material will be necessary to determine a genus and family placement for this taxon.

DISCUSSION

The position of the spermatheca in podotrematous crabs and the gonopores in all crabs, especially on females, has been considered to be of prime importance in the classification and the evolution of the Brachyura (Guinot, 1977; Guinot and Tavares, 2001; Guinot and Quenette, 2005). Recent discoveries from the fossil record have shown that the position of the gonopores and the spermatheca do not always conform to patterns seen in extant specimens. For example, Componocancridae Feldmann et al., 2008, possess an overall primitive sternum, in terms of the shape of the sternites, but the female gonopore is clearly on the sixth sternite, the position seen in the so-called Heterotremata, considered to be a more derived group of brachyurans (Feldmann et al., 2008).

The spermathecae, only present in podotrematous crabs, were described by Guinot and Quenette (2005) as structures lying between the vertical cuticular sheets of the sternites 7 and 8 that extended interiorly into the animal. The spermatheca as far as have been observed are usually located on the suture between the seventh and eighth sternites (Guinot and Quenette, 2005, illustrations), except in Raninidae de Haan, 1839, and *Steorrosia*, discussed below. According to Guinot and Quenette (2005, fig. 14, for example), the spermatheca extend into a tube that presumably helps to hold the sperm plug in place until it is utilized by the female. If the spermatheca is in fact located between two sternites, the tube-like structure would be easily formed between the two vertical sheets of tissue or cuticle between the two sternites. Thus, if the spermathecal opening lies completely on the surface of sternite 7, it would no longer be situated between two cuticular sheets but would be dorsally on top of a sheet of cuticle. The tube therefore could become obsolete and the spermatheca would then simply be a depression to retain the sperm plug, or the tube could migrate to a position within the sternite. The latter is apparently the case in Raninidae (Hartnoll, 1979; Guinot and Quenette, 2005). In Raninidae, the spermatheca are positioned adjacent to one another on sternites 7 along the axis so as to form what appears to be one continuous opening (i.e., Guinot and Quenette, 2005, fig. 24).

Examination of specimens of *Steorrosia pawpawensis* (Fig. 2.3, 2.4) indicates that the external openings of the spermatheca lie entirely on the seventh sternite, a condition rarely observed within Brachyura. The spermathecal opening lies entirely on the seventh sternite and is bounded by the cuticle of the sternite, not by sternal sutures. We know of no other instances in which the spermathecal openings lie entirely on sternite 7 and are not axial. Phylogenetic analysis does not indicate a close relationship between Etyioida and Raninoida; in fact, they are considered as different sections (Karasawa et al., 2011). How did the spermathecal opening migrate from a

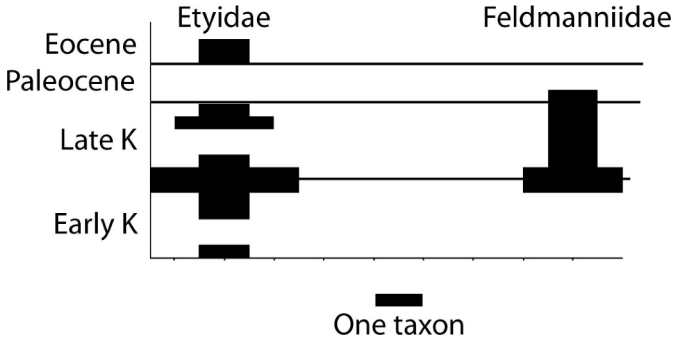

FIGURE 15—Spindle diagrams of the Etyidae and Feldmanniidae, showing distribution of genera through time. Diagram generated using PAST (Hammer et al., 2001).

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position lying along the sternal suture to a position directly upon the sternite? This issue has been deliberated upon by many previous authors (summarized by Guinot and Quenette, 2005). In *Feldmannia* for example, the spermathecal opening is located at the tip of sternite 7, so that it could be an extension of the suture between sternites 7 and 8 but that has rotated anteriorly so as to be an anterior extension of that suture. Further rotation of the opening could result in placement completely on sternite 7. Interestingly, in heterotreme crabs, the gonopore is positioned on the ventral surface of sternite 6, not along a sternal suture. Is this gonopore the migrated gonopore from coxa 3, as has been suggested (Guinot, 1979) or is it a migrated spermatheca from sternite 7? Guinot and Quenette (2005, p. 331, and summarizing many previous authors) suggested that the latter is a difficult scenario to envision.

Karasawa et al. (2011) examined all of the podotrematous brachyurans, long thought to be the most primitive crabs, and also thought to exhibit a relatively small array of body plans based on examination of extant forms (Scholtz and McLay, 2009). Karasawa et al. (2011) found that in fact the Podotremata were polyphyletic, as had been suggested by other phylogenetic studies (Ahyong et al., 2007; Chu et al., 2009; Scholtz and McLay, 2009) and that the carapace morphology and the position of the spermatheca, shape of the sternum, pleon, and pereiopods was quite variable among the Podotremata. In addition to considerable differences in morphology, examination of various lineages of the so-called primitive crabs has revealed that these lineages were remarkably diverse and long-ranging. The Longodromitidae Schweitzer and Feldmann, 2009, initially considered as a primarily Jurassic group (Schweitzer and Feldmann, 2009) is now known to range into the Eocene (Schweitzer and Feldmann, 2011). Many groups of decapods, including Etyidae and Feldmanniidae, survived the end-Cretaceous events only to become extinct later in the Paleocene or Eocene time (Fig. 15). Investigation into these patterns is ongoing.

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