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Revision of the genus *Glyphithyreus* Reuss, 1859 (Crustacea, Decapoda, Brachyura, Xanthoidea) and recognition of a new genus

HIROAKI KARASAWA[1] AND CARRIE E. SCHWEITZER[2]

[1]*Mizunami Fossil Museum, Yamanouchi, Akeyo, Mizunami, Gifu 509-6132, Japan (e-mail: GHA06103@nifty.com)*

[2]*Department of Geology, Kent State University Stark Campus, 6000 Frank Ave. NW, Canton, Ohio 44720 U.S.A. (e-mail: cschweit@kent.edu)*

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Abstract. The definition of the brachyuran genus *Glyphithyreus* Reuss, 1859 (= *Plagiolophus* Bell, 1858 *non* Pomel, 1857) is herein restricted such that the genus now embraces four species ranging from Paleocene to Oligocene in age. Other species previously referred to the genus have been placed in other genera, resulting in one new genus, *Chirinocarcinus*, and four new combinations, *Chirinocarcinus wichmanni* (Feldmann *et al.*, 1995), *Lobonotus sturgeoni* (Feldmann *et al.*, 1995), *Stintonius markgrafi* (Lőrenthey, 1907 [1909]), and *Titanocarcinus bituberculatus* (Collins and Jakobsen, 2003). The referral of *Glyphithyreus* to the Panopeidae Ortmann, 1893, extends the range of that family into the Paleocene. The geographic range of *Stintonius* Collins, 2002, is extended from England to include Egypt as well.

Key words: Brachyura, Decapoda, New taxon, Xanthoidea

Introduction

Glyphithyreus Reuss, 1859, and *Plagiolophus* Bell, 1858, have been problematic since their introduction into the fossil brachyuran (crab) nomenclature. The two genera were named independently for species of fossil brachyurans that are clearly congeneric (see illustrations in Bell, 1858 and Reuss, 1859). Alphonse Milne-Edwards (1865) was the first to recognize this and synonymized the two, indicating that *Plagiolophus* was the senior objective synonym based upon priority. However, Via (1959) subsequently showed that the name *Plagiolophus* had been used by Pomel (1857) for a genus of eutherian mammal, thus rendering *Plagiolophus* Bell a junior homonym of *Plagiolophus* Pomel. *Glyphithyreus* is thus the name with priority for the crab taxon as suggested by Via (1959). All brachyuran species referred to *Plagiolophus* were therefore referred to *Glyphithyreus* as a result of Via's (1959) suggestion. However, some authors maintained the usage of *Plagiolophus* in the literature (Orr and Kooser, 1971; Berglund and Feldmann, 1989) while others used *Glyphithyreus* (Glaessner, 1969; Collins and Morris, 1978; Squires *et al.*, 1992; Feldmann *et al.*, 1995, 1998), contributing to the confusion in usage of the two names.

The situation is made more problematic by the fact that many of the species referred to *Glyphithyreus* (= *Plagiolophus* Bell) over the years are not congeneric with *Glyphithyreus*, at least when compared to the type species, *G. formosus*. It is the purpose of this paper to provide a restricted definition of *Glyphithyreus*, to evaluate each of the species that have been referred to it as well as to *Plagiolophus* Bell, and to recommend generic placement for each (Table 1). This work has resulted in one new genus and four new combinations. Karasawa and Kato's (2003) placement of *Glyphithyreus* within the Eucratopsinae Stimpson, 1871, of the Panopeidae Ortmann, 1893, is supported and extends the range of both the family and subfamily into the Paleocene, as predicted by Casadío *et al.* (in review).

Institutional abbreviations

CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

GMC—Geological Museum Copenhagen, Copenhagen, Denmark

Table 1. All species historically referred to *Glyphithyreus* or *Plagiolophus* and their current generic placement.

Original Placement	Current Placement	Relevant Reference
Glyphithyreus formosus Reuss, 1859 (type species)	*Glyphithyreus*	Reuss, 1859
G. bituberculatus Collins and Jakobsen, 2003	*Titanocarcinus* A. Milne Edwards, 1864	this paper
G. sturgeoni Feldmann *et al.*, 1998	*Lobonotus* A. Milne Edwards, 1864	this paper
?*G. wichmanni* Feldmann *et al.*, 1995	*Chirinocarcinus* new genus	this paper
Plagiolophus ellipticus Bittner, 1875	*Glyphithyreus*	due to synonymy (Via, 1959)
P. wetherelli Bell, 1858 (= *G. affinis* Reuss, 1859)	*Glyphithyreus*	due to synonymy (Via, 1959)
P. sulcatus Beurlen, 1939	*Glyphithyreus*	due to synonymy (Via, 1969)
P. markgrafi Lőrenthey, 1907 [1909]	*Stintonius* Collins, 2002	this paper
P. weaveri Rathbun, 1926	*Orbitoplax* Tucker and Feldmann, 1990	Schweitzer, 2000
P. vancouverensis Woodward, 1896	*Archaeopus* Rathbun, 1908	Glaessner, 1929
P. bakeri Rathbun, 1935	*Lobonotus* A. Milne Edwards, 1864	Via, 1969; Förster, 1970
P. ezoensis Nagao, 1941	*Archaeopus* Rathbun, 1908	Collins, Kanie, and Karasawa, 1993
P. vitiensis Rathbun, 1945	unknown; poorly preserved	examination of holotype, USNM 498430

In.—The Natural History Museum, London, United Kingdom
KSU—Paleontological collections at Kent State University, Kent, Ohio, USA
USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Systematic paleontology

Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Cancroidea Latreille, 1802
Family Cheiragonidae Ortmann, 1893

Included genera.—Erimacrus Benedict, 1892 (extant); *Montezumella* Rathbun, 1930; *Stintonius* Collins, 2002; *Telmessus* White, 1846 (extant).

Diagnosis.—Carapace as long as wide or longer than wide, front bilobed or four-lobed with axial notch; basal antennal article with a triangular projection extending into orbital hiatus; orbits with inner- and outer-orbital spines and median fissure or notch; lateral margins with 4 to 7 spines; posterior quarter of dorsal carapace typically rectangular; posterior margin typically with broad central concavity; sternum with interrupted sutures between sternites 1 and 2 and sternites 2 and 3; complex female genital opening not covered by abdomen.

First pereiopods isochelous; carpus of first pereiopod with spinose outer margin and convex lower margin, usually with a spine; distal margin with two spines; mani of first pereiopods with small spines on outer margin, often in rows (diagnosis after Števčić, 1988; Schweitzer and Salva, 2000).

Genus ***Stintonius*** Collins, 2002

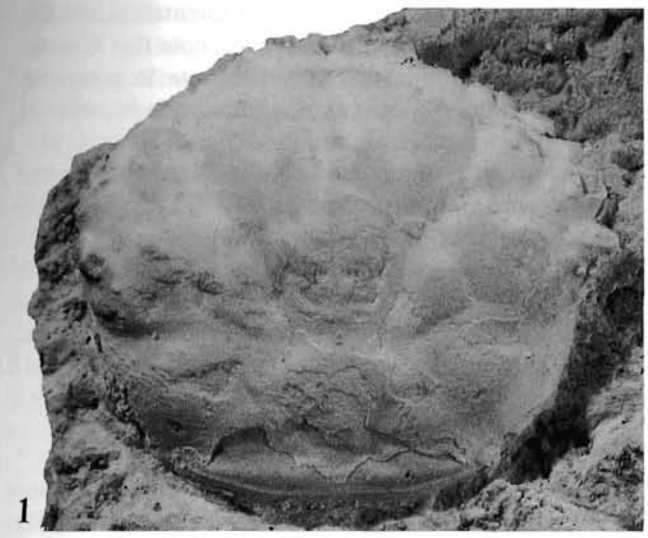
Type species.—Portunites subovata Quayle and Collins, 1981, by monotypy.

Other species.—Stintonius markgrafi (Lőrenthey, 1907 [1909]), as *Plagiolophus.*

Diagnosis.—Carapace longer than wide; anterolateral margin with four spines which become larger posteriorly; carapace regions well defined by narrow grooves; protogastric region long; axial regions long, especially urogastric region; hepatic region reduced; subhepatic region very small; epibranchial region arcuate, comprised of two segments, innermost segment small and triangular; carapace surface appearing to be densely granulate (after Collins, 2002).

Discussion.—Collins (2002) erected the genus *Stintonius* to accommodate the Eocene *Portunites subovata* Quayle and Collins, 1981, subsequent to the suggestion by Schweitzer and Feldmann (1999, 2000) that it did not belong within the genus *Portunites* and may be better placed within the Cheiragonidae. Collins (2002) questionably placed *Stintonius* within the Cheiragonidae, based upon the similarity of

➡ **Figure 1.** Taxa currently or previously referred to *Glyphithyreus* Reuss, 1859. **1.** *Lobonotus sturgeoni* (Feldmann *et al.*, 1998) new combination, dorsal carapace of holotype, CM 36036. **2.** *Glyphithyreus wetherelli* (Bell, 1858), cast of GMC297 currently in KSU collection, KSU 7035. **3.** *Glyphithyreus wetherelli* (Bell, 1858), KSU 4841, Eocene, Sheppey, UK. **4.** *Glyphithyreus wetherelli* (Bell, 1858), KSU 4854, Eocene, Sheppey, UK. **5.** *Glyphithyreus ellipticus* (Bittner, 1875), digital image from Bittner, 1875, plate II, figures 8a and b, a, dorsal view; b, frontal view. **6.** *Glyphithyreus formosus* (Reuss, 1859), digital image from Reuss, 1859, plate II, figure 1. **7.** *Stintonius markgrafi* (Lőrenthey, 1907 [1909]) new combination, digital image from Lőrenthey, 1907 [1909], plate I, fig. 5a. Scale bars = 1 cm.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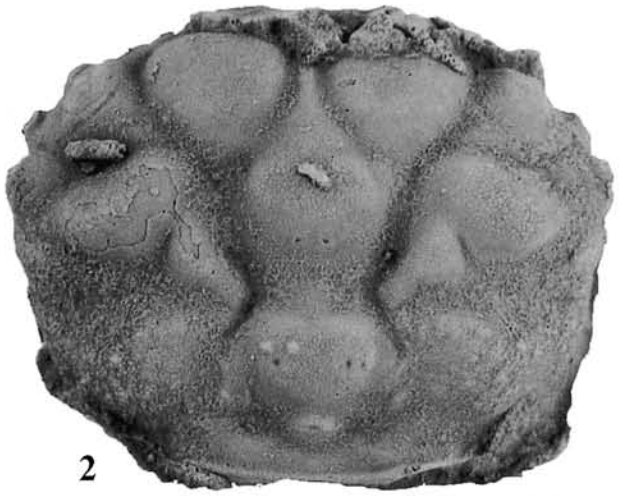
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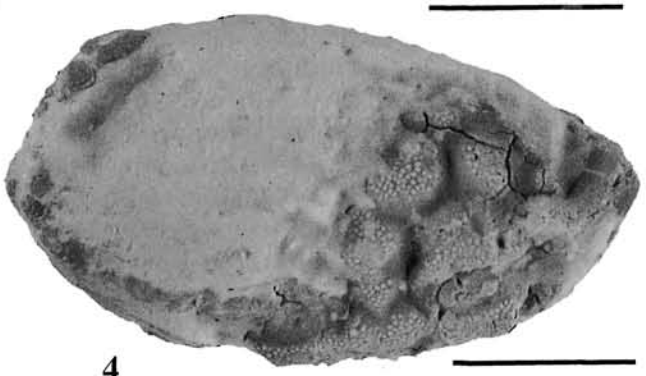
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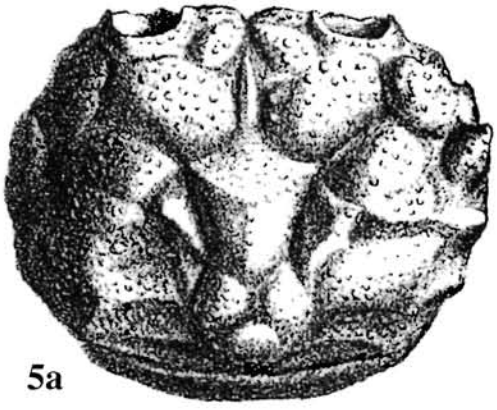
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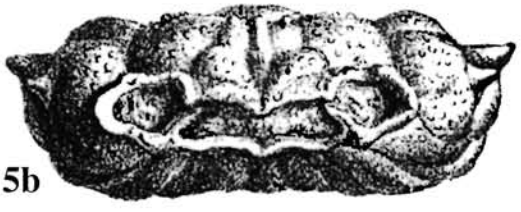
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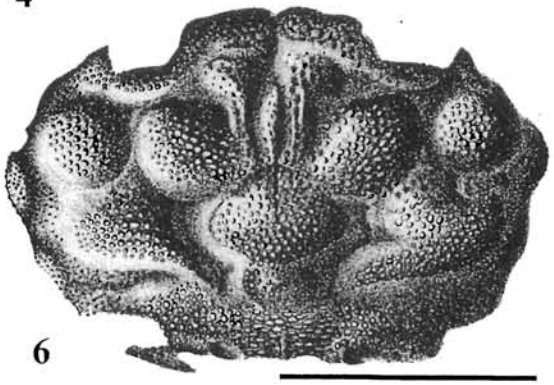
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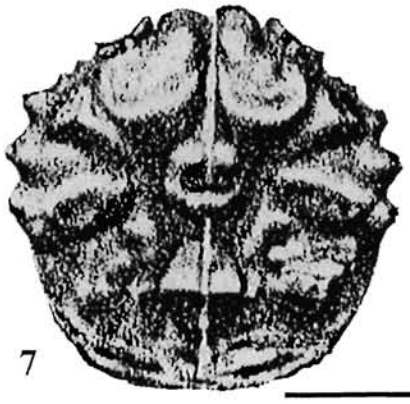
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Stintonius to *Montezumella* Rathbun, 1930, which Schweitzer and Salva (2000) had already placed within the Cheiragonidae. Unfortunately, the specimen of *Stintonius subovata* lacked preserved orbits and frontal margin, which could have facilitated its placement with no reservations into the Cheiragonidae. With the referral of *Plagiolophus markgrafi* to *Stintonius*, it is clear that the genus should definitely be placed within the Cheiragonidae, based upon its bilobed front with axial notch; at least one orbital fissure; inner- and outer-orbital spines; and carapace that is longer than wide. All of these features are diagnostic for the Cheiragonidae (Schweitzer and Salva, 2000). *Plagiolophus markgrafi* has five anterolateral spines, fewer than the extant taxa but one more than *Montezumella*, the only other extinct genus. The referral of *Stintonius* to the Cheiragonidae brings the number of known extinct genera to two; both are Eocene in age.

Stintonius markgrafi (Lőrenthey, 1907 [1909]) new combination

Figure 1.7

Plagiolophus markgrafi Lőrenthey, 1907 [1909], p. 137, pl. 1, figs. 5a, b; Glaessner, 1929, p. 329.

Diagnosis.—Carapace longer than wide, widest at position of last anterolateral spine, about half the distance posteriorly on carapace; front bilobed with axial notch; inner- and outer-orbital spines well developed, orbits with at least one fissure; regions well developed; hepatic and branchial regions with oblique, ridgelike ornamentation; anterolateral margin with 5 spines excluding outer-orbital spine.

Discussion.—*Plagiolophus markgrafi*, described from the Eocene of Egypt (Lőrenthey, 1907 [1909]), cannot be accommodated by *Glyphithyreus* (=*Plagiolophus*) for several reasons. The carapace of *P. markgrafi* is longer than wide, not wider than long as in *Glyphithyreus*, and *P. markgrafi* lacks the transverse ridges separated by deeply depressed areas on the branchial regions that typify *Glyphithyreus*. The shape and development of carapace regions; the longer than wide carapace; the bilobed nature of the front, also with an axial notch; the presence of orbits with fissures and inner- and outer-orbital spines; the rectangular posteriormost end of the carapace; and the possession of between 4 and 7 (5 in *P. markgrafi*) anterolateral spines indicate that *P. markgrafi* is a member of the Cheiragonidae.

Of the two known Eocene genera, *Stintonius* can best accommodate *P. markgrafi* due to its possession of tumid, well defined regions, which *Montezumella* lacks, and its lack of scabrous ornamentation, which is typical of *Montezumella*. However, note that *S. markgrafi* differs from *Stintonius subovata* in possessing oblique, ridgelike ornamentation on the hepatic and branchial regions. Examination of type material of *S. markgrafi* may suggest that it should be referred to a cheiragonid genus distinct from both *Montezumella* and *Stintonius*.

Stintonius is now known from Eocene rocks of England and Egypt.

Superfamily Xanthoidea MacLeay, 1838
Family Panopeidae Ortmann, 1893
Subfamily Eucratopsinae Stimpson, 1871

Discussion.—*Glyphithyreus* had previously been placed within the subfamily Carcinoplacinae H. Milne Edwards, 1852, of the family Goneplacidae (Balss, 1957; Glaessner, 1969; and many subsequent workers). *Glyphithyreus* has well defined dorsal carapace regions, which is not typical of the Goneplacidae. *Glyphithyreus* lacks a straight frontal margin without a median notch, an entire upper orbital margin with an indistinct supraorbital angle, and a wide male abdomen with all free somites; all of these features are diagnostic characters of the subfamily Goneplacinae MacLeay, 1838 (= Carcinoplacinae) *sensu* Karasawa and Kato, 2003. Thus, Karasawa and Kato (2003) removed *Glyphithyreus* from the Goneplacinae of the Goneplacidae to the panopeid subfamily Eucratopsinae Stimpson, 1871, because the carapace has well defined dorsal regions, the front consists of two rounded lobes, and the narrow male abdomen has fused somites 3–5.

Distinction between the panopeid eucratopsine genera and members of the Pseudorhombilidae is difficult based upon characters of the carapace, thoracic sternum, male abdomen, and pereiopods. Major differences between extant forms are only in the morphology of the male gonopods (Hendrickx, 1998). Recently, Schweitzer and Karasawa (2004) indicated that the fronto-orbital width to carapace width ratio and the frontal width to carapace width ratio in the Eucratopsinae are consistently higher than in the Pseudorhombilidae Alcock, 1900, and redefined both taxa. The fronto-orbital width to maximum carapace width ratio in the Eucratopsinae is about 63–81 percent while in the Pseudorhombilidae it is about 53–59 percent. The frontal width in the Eucratopsinae occupies about 30 to 43 percent of the maximum carapace width but in the Pseudorhombilidae it is about 26–32 percent of the maximum carapace width. In *Glyphithyreus* the fronto-orbital width to maximum carapace

width ratio is about 63–70 percent and the frontal width to maximum carapace width ratio is about 30–33 percent. Thus, the placement of *Glyphithyreus* in the Eucratopsinae is acceptable.

Because *Glyphithyreus* is known from the Paleocene of Pakistan (Collins and Morris, 1978), it is thus the earliest known occurrence of the family and subfamily. The Panopeinae Ortmann, 1893, was previously known to have a well established Eocene record (Casadío *et al.*, in review). The supposition by Casadío *et al.* (in review) that the Panopeinae and the Eucratopsinae diverged sometime before the Eocene is therefore supported.

Genus ***Glyphithyreus*** Reuss, 1859
(= *Plagiolophus* Bell, 1858 *non* Pomel, 1857)

Figure 1.2–1.6

Glyphithyreus Reuss, 1859, p. 4, pl. 2, figs. 1–3.
Plagiolophus Bell, 1858, p. 19, pl. II, figs. 7–13 (*nom. preoccup.* by *Plagiolophus* Pomel, 1857).

Type species.—*Plagiolophus wetherelli* Bell, 1858 = *Glyphithyreus affinis* Reuss, 1859, by monotypy under ICZN, 1999, Article 67.8.

Species included.—*Glyphithyreus ellipticus* (Bittner, 1875) as *Plagiolophus*, *G. formosus* Reuss, 1859; *G. sulcatus* (Beurlen, 1939), as *Plagiolophus*; *G. wetherelli* (Bell, 1858), as *Plagiolophus* (= *G. affinis* Reuss, 1859).

Diagnosis.—Carapace subquadrilateral, wider than long, L/W about 0.75–0.80, widest in anterior one-third of carapace; fronto-orbital margin about 63–70 percent maximum carapace width; front comprised of two slightly rounded lobes, about one-third maximum carapace width, with median notch; supraorbital angle weakly defined; upper orbital margin concave, rimmed, weakly notched medially or with two fissures; anterolateral margin strongly convex with four spines including outer-orbital spine, third spine largest; posterolateral margin sinuous, converging posteriorly; regions granular dorsally, well defined by deep, smooth grooves; epigastric regions well defined; mesogastric region separated from metagastric region by V-shaped groove; each epibranchial region inflated with broad ridge forming convex-forward arc from metagastric region to last anterolateral spine; broad transverse ridge across cardiac and metabranchial regions, forming nearly continuous ridge across carapace; epibranchial and cardiac/metabranchial ridges separated by deep cavity; posterior end of carapace depressed to level of cavity separating two branchial ridges.

Thoracic sternum relatively wide; male abdomen narrow with somites 3–5 fused. Chelipeds massive, elongate.

Discussion.—Bell (1858) described a new genus and species, *Plagiolophus wetherelli*, from the Eocene London Clay of England. Reuss (1859) described a new genus, *Glyphithyreus*, and two new species, *G. formosus*, the type species, and *G. affinis*. Alphonse Milne Edwards (1865) synonymised *Glyphithyreus affinis* Reuss, 1859, with *P. wetherelli*, and indicated that *Glyphithyreus* was the junior subjective synonym of *Plagiolophus*. Via (1959) showed that the generic name *Plagiolophus* was preoccupied by *Plagiolophus* Pomel, 1857, for a genus of Mammalia, and first used the junior subjective synonym of the valid name, *Glyphithyreus* Reuss, 1859, instead of *Plagiolophus* Bell, 1858. We concur with Via's (1959) decision.

Glaessner (1929) recognized four species of *Plagiolophus* (= *Glyphithyreus*), *P. ellipticus* Bittner, 1875; *P. markgrafi* Lőrenthey, 1907 [1909]; *P. weaveri* Rathbun, 1926; and *P. wetherelli*, the latter of which he considered to be synonymous with both *G. affinis* Reuss, 1859, and *G. formosus* Reuss, 1859. Glaessner (1929) also moved *P. vancouverensis* Woodward, 1896, to *Archaeopus* Rathbun, 1908, of the family Retroplumidae Gill, 1894. Four additional species, *Plagiolophus bakeri* Rathbun, 1935, from the Eocene of U.S.A.; *P. ezoensis* Nagao, 1941, from the Cretaceous of Japan; *P. sulcatus* Beurlen, 1939, from the Oligocene of Hungary; and *P. vitiensis* Rathbun, 1945, from the Miocene of Fiji, were subsequently described. In his review of the Eocene decapods of the world, Via (1969) placed *P. ellipticus*, *P. ezoensis*, *P. markgrafi*, *P. sulcatus*, *P. weaveri*, and *P. vitiensis* within *Glyphithyreus*. Both Via (1969) and Förster (1970) moved *Plagiolophus bakeri* to *Lobonotus* A. Milne Edwards, 1864, of the family Xanthidae MacLeay, 1838; we concur. *Lobonotus* is now placed within the Pilumnidae Samouelle, 1819 (Schweitzer *et al.*, 2004).

More recently, *Glyphithyreus ezoensis* was assigned to the retroplumid genus *Archaeopus* Rathbun, 1908 (Collins, Kanie, and Karasawa, 1993). *Glyphithyreus weaveri* was moved to *Orbitoplax* Tucker and Feldmann, 1990, of the family Goneplacidae MacLeay, 1838 (Schweitzer, 2000). Collins and Morris (1978) described *G. wetherelli* from the Paleocene of Pakistan and treated *G. formosus* as a valid species, with which we concur. The specimen they assigned to *G. wetherelli* conforms to the general diagnosis of *Glyphithyreus* in possessing broad orbits and marked transverse ridges on the dorsal carapace; thus, it is the earliest known occurrence of the genus.

The only known Miocene species of *Glyphithyreus*,

Glyphithyreus vitiensis, is here excluded from the genus because it lacks branchial ridges (USNM 498430), which are diagnostic characters of the genus. *Glyphithyreus vitiensis* possesses carapace characters most like those of *Xanthodius kambaraensis* Rathbun, 1945 (Xanthidae), from the Miocene of Fiji. In recent works, *Glyphithyreus sturgeoni* Feldmann *et al.*, 1998, from the Eocene of U.S.A. and ?*G. wichmanni* Feldmann *et al.*, 1995, from the Danian of Argentina, have been described. However, both species lack very distinctive branchial ridges, which are typical of *Glyphithyreus*, and they are assigned to other genera described below.

Consequently, we recognize only four species of *Glyphithyreus* (Table 1). Of these, the placement of *G. sulcatus* is somewhat tentative and is based upon our translation of Beurlen's (1939) original description in German and the very poorly reproduced illustration in our copy of the work. The description of *G. sulcatus* clearly indicates two transverse ridges on the branchial regions, separated by a very deep cavity, which is certainly characteristic of *Glyphithyreus*. Thus we place the species in the genus until type material can be examined. *Glyphithyreus wetherelli* is recorded from the Paleocene of Pakistan (Collins and Morris, 1978) and the Eocene of England, Belgium, Denmark, France, Spain, and Senegal (Bell, 1858; Remy *in* Remy and Tessier, 1954; Via, 1969; Plaziat and Secretan, 1971). *Glyphithyreus wetherelli* recorded from Denmark (Ravn, 1903; Via, 1969; Plaziat and Secretan, 1971) was assigned to the new species, *Glyphithyreus bituberculatus* (as *Titanocarcinus bituberculatus* in this paper), by Collins and Jakobsen (2003). *Glyphithyreus ellipticus* is only known from the Eocene of Italy (Bittner, 1875), and *Glyphithyreus formosus* is from the Cretaceous? of Germany (Reuss, 1859). Thus, *Glyphithyreus* is generally known from Paleocene and Eocene deposits in the western Tethys realm.

Family Goneplacidae MacLeay, 1838
?Subfamily Euryplacinae Stimpson, 1871

Diagnosis.—Carapace usually with poorly defined carapace regions; front straight with shallow median notch; supraorbital angle distinct; orbit sometimes deep, large, with two, one or no orbital fissures; anterolateral margin with two to five spines (after Karasawa and Kato, 2003, p. 138–139). For remainder of diagnosis, see Karasawa and Kato (2003).

Discussion.—The general shape of the carapace and carapace regions; the spined nature of the anterolateral margins; and the clear distinction between the anterolateral and posterolateral margins all indicate that ?*Glyphithyreus wichmanni* is a member of the Xanthoidea. Paleocene xanthoids are relatively uncommon, although they have received directed attention in recent years (Schweitzer, 2003a, b, in press).

A major problem for family, subfamily, and generic placement of ?*Glyphithyreus wichmanni* is that the ventral aspects of the carapace are unknown. Features of the sternum, abdomen, and articulation of the pereiopods are very important in xanthoid classification of both extant and fossil members (Guinot, 1978; Davie, 2002; Karasawa and Kato, 2003; Schweitzer, 2003a, b, in press). Thus, proxy characters of the dorsal carapace (Schweitzer and Feldmann, 2000; Schweitzer, 2003a) must be used. The short anterolateral margin relative to the posterolateral margin clearly excludes ?*G. wichmanni* from genera within the Palaeoxanthopsidae Schweitzer, 2003a, and the Zanthopsidae Via, 1959, both xanthoid families with Paleocene representatives. The Hexapodidae Miers, 1886, have a fossil record extending into the Cretaceous (Schweitzer, in press), but the distinctively rectangular carapace and carapace dimensions of the embraced genera (Schweitzer and Feldmann, 2001) cannot accommodate ?*G. wichmanni.*

?*Glyphithyreus wichmanni* cannot be accommodated by the Eriphiidae MacLeay, 1838, because members of that family have either very broad frontoorbital widths, occupying most of the maximum carapace width, or two orbital fissures, neither of which ?*G. wichmanni* possesses. The Trapeziidae Miers, 1886, possess very broadly spaced orbits and smooth dorsal carapaces which cannot accommodate ?*G. wichmanni.* Similarly, the smooth dorsal carapace and very long, convex anterolateral margins of the Carpiliidae Ortmann, 1893, cannot embrace ?*G. wichmanni.* Members of the Pseudorhombilidae Alcock, 1900, have two orbital fissures and an intraorbital spine, none of which ?*G. wichmanni* possesses. Taxa within the Platyxanthidae Guinot, 1977, possess two orbital fissures and a more narrow front and a wider carapace relative to the length than does ?*G. wichmanni.* The Pseudoziidae Alcock, 1898, are much wider than long and have poorly defined regions, while ?*G. wichmanni* is only slightly wider than long (L/W = 0.83), and has well defined regions. Members of the Xanthidae MacLeay, 1838 sensu stricto have long anterolateral margins and concave posterolateral margins, neither of which ?*G. wichmanni* exhibits. ?*Glyphithyreus wichmanni* has very much shorter anterolateral margins than is typical of members of the Panopeidae Ortmann, 1893, and its regions are in general better developed than in members of the Panopeidae. In

addition, at least some panopeids have two orbital fissures, which ?*G. wichmanni* lacks.

The two families to which ?*G. wichmanni* is most likely referable are the Pilumnidae Samouelle, 1819, and the Goneplacidae MacLeay, 1838. Members of the Goneplacidae usually have very short anterolateral margins, a prominent character displayed by ?*Glyphithyreus wichmanni*. In addition, the Goneplacidae is one of the few xanthoid families with a fossil record extending into the Cretaceous (Schweitzer *et al.*, 2002), and which can therefore accommodate ?*G. wichmanni* without a range extension. The goneplacid subfamily Euryplacinae Stimpson, 1871, as defined by Karasawa and Kato, 2003, is quite variable in terms of dorsal carapace morphology. Some genera possess two orbital fissures, for example, *Viaplax* Karasawa and Kato, 2003; some possess one orbital fissure, for example, *Stoaplax* Vega *et al.*, 2001; while others possess none, as in *Orbitoplax* Tucker and Feldmann, 1990. The dorsal carapace regions of species of *Orbitoplax* are very well defined, while those of *Stoaplax* are not, and extant genera such as *Nancyplax* Lemaitre *et al.*, 2001, are nearly smooth. In spite of this variability, all euryplacines possess short anterolateral margins and relatively broad fronto-orbital widths, which can accommodate ?*G. wichmanni*. In addition, euryplacines possess from two to five anterolateral spines, a well defined supraorbital angle, and relatively large orbits, all of which can accommodate ?*G. wichmanni*. The front of ?*G. wichmanni* appears to be notched medially, another feature typical of euryplacines. Thus, the Euryplacinae can best accommodate ?*G. wichmanni*, for which a new genus has been erected below, and we tentatively place it within the Euryplacinae until aspects of the sternum, abdomen, and pereiopods can be examined.

Other subfamilies of the Goneplacidae cannot accommodate ?*Glyphithyreus wichmanni*. Members of the Goneplacinae MacLeay, 1838, usually have broad orbits and narrow fronts, not exhibited by ?*G. wichmanni*. The Carinocarcinoidinae Karasawa and Kato, 2003, possess transverse keels on a relatively smooth dorsal carapace; neither are seen in ?*G. wichmanni*. The Chasmocarcininae Serène, 1964 and Trogloplacinae, Guinot, 1986, are typified by rectangular, relatively featureless dorsal carapaces, which cannot accommodate ?*G. wichmanni*. Fossil taxa within the Mathildellinae Karasawa and Kato, 2003, have flattened carapaces, two orbital fissures, and moderate fronto-orbital widths of about half the carapace width, none of which ?*G. wichmanni* possesses; however, the arrangement of carapace regions in both *Tehuacana* Stenzel, 1944, and *Branchioplax* Rathbun, 1916, is similar to that of ?*G. wichmanni*.

Members of most subfamilies of the Pilumnidae have very unusual shapes (Halimedinae Alcock, 1898; Calmaniinae Števčić, 1991; Eumedoninae Dana, 1853; Rhizopinae Stimpson, 1858; see Davie, 2002) which exclude ?*G. wichmanni*. The general arrangement of carapace regions and proportions of the carapace in ?*G. wichmanni* are similar to that seen in the Pilumninae Samouelle, 1819. The Galeninae Alcock, 1898, a monogeneric subfamily, have poorly defined carapace regions and a very broad carapace as compared to the length, not seen in ?*G. wichmanni*. Members of both the Pilumninae and the Galeninae have longer anterolateral margins than does ?*G. wichmanni*. In addition, the orbits of most pilumnines are directed anterolaterally, while those of ?*G. wichmanni* are directed forward. Thus, it is most likely that ?*G. wichmanni* is not a member of the Pilumnidae.

Chirinocarcinus new genus

Glyphithyreus Reuss, 1859 (part). Feldmann, Casadío, Chirino-Galvez, and Aguirre-Urreta, 1995, p. 14, figs. 11, 12.

Type species.—?*Glyphithyreus wichmanni* Feldmann, Casadío, Chirino-Galvez, and Aguirre-Urreta, 1995, by monotypy.

Diagnosis.—Carapace slightly wider than long, L/W about 0.83, widest at position of last anterolateral spine about one-third the distance posteriorly on carapace; front appearing to have axial notch, about 35 percent maximum carapace width, projecting beyond orbits; orbits circular, entire, directed forward, outer-orbital angle projecting slightly; fronto-orbital width about 63 percent maximum carapace width; anterolateral margin very short, with three spines excluding outer-orbital spine, last spine largest; posterolateral margin long, sinuous, convex; posterolateral reentrants well developed; posterior margin short, concave; carapace regions developed as broadly swollen areas separated by relatively deep grooves; urogastric and cardiac regions ornamented with tubercles.

Etymology.—The genus name honors Luis Chirino-Gálvez, Chile, formerly a graduate student at Kent State University, Kent, Ohio, who has contributed much to our understanding of fossil crabs from South America, especially those of Chile.

Discussion.—*Glyphithyreus wichmanni*, questionably referred to *Glyphithyreus* by Feldmann *et al.* (1995), cannot be retained within that genus. The type species of *Glyphithyreus*, *G. wetherelli* (Bell, 1858), exhibits very distinctive, transverse ridges on the dorsal carapace. These ridges are composed of the

arcuate epibranchial regions, which are linearly and transversely swollen, and transverse ridges on the mesobranchial region, which are nearly continuous with the transversely swollen cardiac region. ?*Glyphithyreus wichmanni* lacks these transverse ridges. *Glyphithyreus wetherelli* has two orbital fissures, observed on In. 59575 and In. 48229, while *G. wichmanni* lacks orbital fissures. *Glyphithyreus wetherelli* has five anterolateral spines, while *G. wichmanni* has only three. *Glyphithyreus wichmanni* is more equant than *G. wetherelli*, which is markedly wider than long. Thus, ?*G. wichmanni* must be removed from *Glyphithyreus*.

We herein place ?*Glyphithyreus wichmanni* in a new genus, tentatively within the Euryplacinae, resulting in the new combination *Chirinocarcinus wichmanni*. Of the three fossil genera previously referred to that subfamily (Karasawa and Kato, 2003), ?*G. wichmanni* lacks orbital fissures, which are present in the extinct genera *Stoaplax* and *Viaplax*, and absent in *Orbitoplax*. *Chirinocarcinus* has moderately large orbits, as in *Viaplax*, instead of very large orbits, as in *Orbitoplax* and *Stoaplax*. No other fossil genus has this particular combination of orbital fissures and orbit size. In addition, the dorsal carapace of *Chirinocarcinus* is more equant than members of *Orbitoplax*, and the orbits of *Orbitoplax* and *Stoaplax* are rectangular and very deep, not seen in *Chirinocarcinus*. If *Chirinocarcinus* is confirmed as a member of the subfamily, it would be the oldest member known, Paleocene in age, whereas the other fossil taxa are Eocene.

Family Pilumnidae Samouelle, 1819
Genus ***Lobonotus*** A. Milne Edwards, 1864

Type species.—*Lobonotus sculptus* A. Milne Edwards, 1864, by monotypy.

Other species.—*Lobonotus bakeri* (Rathbun, 1935), as *Plagiolophus*; *L. brazoensis* Stenzel, 1935 (known only from claws); *L. mexicanus* Rathbun, 1930; *L. natchitochensis* Stenzel, 1935; *L. sandersi* (Blow and Manning, 1997), as *Eohalimede* Blow and Manning, 1997; *L. sturgeoni* (Feldmann *et al.*, 1998) as *Glyphithyreus*.

Diagnosis.—see Schweitzer *et al.* (2004).

Discussion.—Schweitzer *et al.* (2002) examined the genus *Lobonotus* and removed some species from it, and they also referred *Eohalimede sandersi* Blow and Manning, 1997, to the genus. Schweitzer *et al.* (2004) restricted the genus to those species listed above, other than *L. sturgeoni*. They placed *Lobonotus* within the Pilumnidae based upon features of the sternum, male abdomen, and dorsal carapace. *Lobonotus lobulata* Feldmann *et al.*, 1995, and *Lobonotus orientalis* Collins and Morris, 1978, were each removed to new genera, *Lobulata* and *Pakicarcinus* respectively (Schweitzer *et al.*, 2004). These actions restricted the genus to only Central and North American forms; the referral herein of *Glyphithyreus sturgeoni*, described from the Eocene of North Carolina, USA, to the genus maintains this geographic pattern. All of the known occurrences, except for the Miocene *L. sculptus*, are from Eocene rocks (Schweitzer *et al.*, 2002).

Lobonotus sturgeoni (Feldmann, Bice, Schweitzer Hopkins, Salva, and Pickford, 1998) new combination

Fig. 1.1

Glyphithyreus sturgeoni Feldmann, Bice, Schweitzer Hopkins, Salva, and Pickford, 1998, p. 13, figs. 17, 18.

Diagnosis.—Carapace length nearly 90 percent width, small for genus; front axially notched, with six small protuberances including inner orbital protuberance; orbits broadly rimmed, with two well developed fissures; anterolateral margin with 4 spines excluding outer orbital spine; carapace regions well marked by deep grooves; surface of carapace coarsely granular, especially near lateral margins; cardiac region weakly three-lobed.

Material examined.—CM 36036, holotype.

Discussion.—*Glyphithyreus sturgeoni* is here referred to the genus *Lobonotus* due to its possession of numerous dorsal carapace characters similar to those of the type species. These features include an equant carapace that is steeply vaulted anteriorly; a notched front; orbits with two well developed fissures; deep grooves and well developed regions ornamented with granules; anterolateral margin with 4 spines; and a weakly three-lobed cardiac region. All of these features are diagnostic for the genus. *Lobonotus sturgeoni* may be differentiated from other species of the genus by its small size (17.3 mm wide versus nearly 40 mm in *Lobonotus mexicanus* in Schweitzer *et al.*, 2002). The cardiac region of *L. sturgeoni* is more weakly trilobed than in other members of the genus, and the ornamentation appears to be less dense than in other species. However, as the specimen is a mold of the interior, much surface detail has probably been lost. The front of *Lobonotus sturgeoni* clearly exhibits six weak protuberances, which have not been described in other species; the front typically has been described as nearly straight. All of these differences are clearly within the range of generic variation; the species is referred to *Lobonotus* with no reservations.

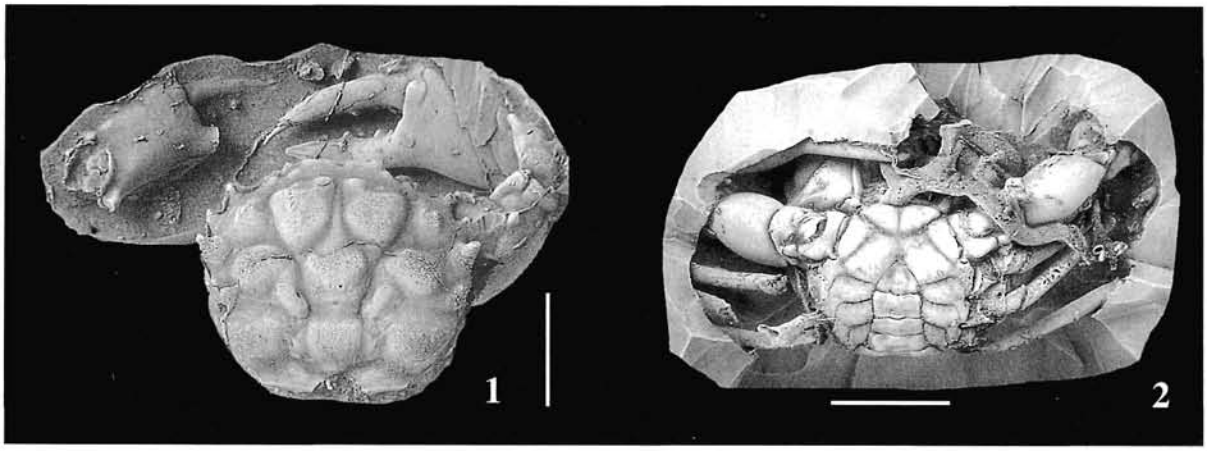

Figure 2. *Titanocarcinus bituberculatus* (Collins and Jakobsen, 2003) new combination. **1**. Reproduced figure of plate 5, figure 2a, from the Bulletin of the Mizunami Fossil Museum. **2**. Reproduced figure of plate 5, figure 5b, from the Bulletin of the Mizunami Fossil Museum. Scale bars = 1 cm.

Genus ***Titanocarcinus*** A. Milne Edwards, 1864

Type species.—*Titanocarcinus serratifrons* A. Milne Edwards, 1864, by subsequent designation of Glaessner (1929).

Discussion.—*Glyphithyreus bituberculatus* Collins and Jakobsen, 2003, cannot be accommodated by *Glyphithyreus* because it lacks the branchial ridges separated by a deep cavity and the very depressed posteriormost end of the carapace diagnostic for *Glyphithyreus*. It most closely resembles species of *Titanocarcinus*, based upon its notched front; rimmed orbits with two fissures; well developed carapace regions separated by broad, smooth grooves; epibranchial region well subdivided into two areolae; equant carapace; and anterolateral margins with three spines.

Collins and Morris (1978) suggested that *Titanocarcinus* might be synonymous with *Lobonotus*; Schweitzer *et al.* (2002) concurred. Schweitzer *et al.* (2004) reevaluated *Lobonotus* but did not make a decision on the *Lobonotus* and *Titanocarcinus* issue. Such a decision is beyond the scope of this paper but is being considered by the authors. For now, we place the Paleocene *Glyphithyreus bituberculatus* in *Titanocarcinus* based upon its possession of only three anterolateral spines, as in *T. serratifrons*, the type species, and *T. raulinensis* A. Milne Edwards, 1864; and a cardiac region that is very weakly trilobed. Species referred to *Lobonotus* have four or five anterolateral spines and distinctly trilobed cardiac regions. However, species of *Titanocarcinus* usually have a longitudinal groove in the protogastric region, which *G. bituberculatus*, as well as species of *Lobonotus*, lack. Historically, European species have been referred to *Titanocarcinus* and American forms have been referred to *Lobonotus* (Collins and Morris, 1978; Schweitzer *et al.*, 2002); we follow that precedent for the time being. As currently defined, *Titanocarcinus* is known from Cretaceous to Miocene rocks (Glaessner, 1969).

Titanocarcinus bituberculatus (Collins and Jakobsen, 2003) new combination

Figure 2.1, 2.2

Glyphithyreus bituberculatus Collins and Jakobsen, 2003, p. 74, fig. 6, pl. 5, figs. 1–5.

Diagnosis.—Carapace not much wider than long, widest just posterior to last anterolateral spine; front notched, about one-third maximum carapace width; orbits rimmed, with two fissures; fronto-orbital width about two-thirds maximum carapace width; anterolateral margins with three spines excluding outer-orbital spines; carapace regions well developed, separated by broad, smooth grooves.

Sternum ovate; sternites 1–2 fused, no evidence of suture; strong, entire groove marking suture between sternites 2 and 3; very deep groove between sternites 3 and 4, medially interrupted; sternite 4 with deep grooves marking fusion of episternites of sternite 3 with sternite 4; deep groove extending anteriorly from sterno-abdominal cavity onto sternites 4 and 3; male abdomen possibly covering entire space between coxae of pereiopods 5, but unable to determine for certain; all male abdominal somites free.

Discussion.—Schweitzer *et al.* (2004) described the male abdomen of species of *Lobonotus* as not entirely covering the space between the coxae of pereiopods 5, based upon examination of the type of *L. mexicanus* Rathbun, 1930 (USNM 371096). A small portion of sternite 8 may have been exposed, but that area of the specimen is covered with sediment that cannot be prepared away. In the specimens of *T. bituberculatus*, it is difficult to determine what the relationship between the male abdomen and the coxae of the fifth pereiopods was, as those coxae are not preserved; the male abdomen is broadened in that region, suggesting that it may have filled the entire space between those coxae. However, it is not possible to know for certain and it is similarly not possible to know if any portion of sternite 8 was visible in *T. bituberculatus*. If the male abdomen of *T. bituberculatus* did in fact fill the entire space between the coxae of the fifth pereiopods, the apparent relationship between *Lobonotus* and *Titanocarcinus* becomes problematic because these features of the male abdomen and sternum are considered to be extremely important at the genus, subfamily, and family level. If *Titanocarcinus* and *Lobonotus* were to be synonymized, these possible differences would have to be taken into account.

The deep sternal grooves of *T. bituberculatus* certainly suggest affinity with members of a new family (Schweitzer, in press) or Zanthopsidae Via, 1959. Schweitzer (in press) suggested that these deep grooves may be a primitive feature among some Xanthoidea, as they appear in many Eocene taxa as well as the Platyxanthidae Guinot, 1977, which was considered by Guinot (1978) to possess many plesiomorphic characters. Similar groove patterns are found in some members of various subfamilies of the Pilumnidae; perhaps they are plesiomorphic characters retained by some members of the family. Investigation of these groove patterns is ongoing.

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