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WHAT IS *CANCER*?

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ABSTRACT

Cancer is one of the "oldest" names in carcinology, but like many old and familiar things it has fallen into use as a catch-all category, especially by non-taxonomists. Much taxonomic revision has occurred in Brachyura: Cancridae [*Cancer*] in recent years, and unfortunately, much of it has passed completely under the radar of biologists. A summary of that revisionary work is provided along with a list of currently accepted names for the living species of Cancridae. We offer this contribution in an effort to cut off the use of old, and in many cases invalid, binomina, and to encourage the use of a modern, up-to-date classification of cancrid crabs.

KEY WORDS: *Cancer*, Cancridae, nomenclature

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INTRODUCTION

The name *Cancer* Linnaeus, 1758, is amongst the oldest of generic nomina in zoology. At its inception, it was virtually synonymous with "Crustacea." However, it quickly came to be recognized by early naturalists that *Cancer* as Linnaeus originally conceived it, held a variety of diverse and unrelated taxa, and eventually by the time of Latreille (1802) the name came to signify a particular kind of brachyuran crab.

As knowledge of the biodiversity and morphological disparity of crabs evolved, a superfamily Cancroidea Latereille, 1802, was eventually recognised, and includes at present three families: Atelecyclidae Ortmann, 1893; Cancridae Latreille, 1802; and Pirimelidae Alcock, 1899 (Ng et al., 2008). Two other families, Cheiragonidae Ortmann, 1893, and Corystidae Samoulle, 1819, may be closely related to Cancridae (Schweitzer and Feldmann, 2010) but are currently placed in their own superfamilies until their affinities are better understood (Ng et al., 2008).

Taxonomies fulfil two separate and distinct roles, a point many people often lose sight of: 1) as simple catalogues to track names and approximate species concepts (what most museum curators and non-taxonomists are interested it), and 2) as natural systems that reflect phylogenetic relationships. Sometimes, trying to reconcile these two roles becomes vexing. A recent example involves the dendrobranchiate prawn genus *Penaeus* Fabricius, 1798. Sorting out the phylogenetic relationships in Penaeidae is an on-going challenge (see Burkenroad, 1983; Tavares and Martin, 2011), but Pérez-Farfante and Kensley (1997) achieved a substantial benchmark when they formally reorganized an array of old, and created some new, genera to arrive at a natural synthesis of penaeid taxonomy. Their analysis of penaeid classification remains the most complete and detailed morphological analysis yet conducted, and their resulting hypothesis is not only academically sound but also highly testable. The resulting outcry from the fishery community continues (see Dall, 2007), with protests against both the loss of those old familiar names, and over conflicting patterns from molecular and morphological analyses (see Lavery et al., 2006; Flegel, 2007; McLaughlin et al., 2007; Ma et al., 2009). That brouhaha still rages. This "mess," as some carcinologists have called this development, is, however, not a mess at all. It results from confusing how science works, i.e., hypotheses constantly changing in light of new evidence, and practical here-and-now day-by-day needs that require constancy and familiarity.

HISTORY OF THE NAME *Cancer*

The genus *Cancer* is familiar to every student who has taken a marine invertebrates course in the West. Since the days of Linnaeus, the continuous descriptions of species of *Cancer* have resulted in a long list of taxa. Even so, diversity within *Cancer* began to be recognized rather early. Alphonse Milne-Edwards (1862) erected the genus *Metacarcinus* for the well-known American species, *Cancer magister* Dana, 1852. Rathbun (1906) created the genus *Platepistoma* as a monotypic genus to accommodate *P. macrophthalmus* Rathbun, 1906, from Hawai'i. Nevertheless, these efforts were generally ignored as new living and fossil species continued to be recognized as members of *Cancer*.

One cannot ignore the importance of the fossils in this on-going effort to understand this genus. Nations (1975) in an important monograph recognized four subgenera: *Can-*

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cer (sensu stricto) Linnaeus, 1758; *Glebocarcinus* Nations, 1975; *Metacarcinus* A. Milne-Edwards, 1862; and *Romaleon* Gistel, 1848. Nations did not recognize Rathbun's *Platepistoma*, but Davie (1991) argued that the genus was valid, described three new species, and included some taxa previously thought to have been species of *Cancer*.

The fossils continued to play an important role as seen in the work of Schweitzer and Feldmann (2000), who incorporated earlier recognized fossil species and erected three new genera to accommodate fossil taxa from North and South America. Within a subfamily Cancrinae Latreille, 1802, they included *Anatolikos* Schweitzer and Feldmann, 2000; *Anisospinos* Schweitzer and Feldmann, 2000; *Cancer* Linnaeus, 1758; *Glebocarcinus* Nations, 1975; *Metacarcinus* A. Milne-Edwards, 1862; *Notocarcinus* Schweitzer and Feldmann, 2000; *Platepistoma* Rathbun, 1906; and *Romaleon* Gistel, 1848. An extinct subfamily Lobocarcininae Beurlen, 1930, contains three genera: *Lobocarcinus* Reuss, 1857; *Miocyclus* Müller, 1979; and *Tasadia* Müller, 1884.

From the above, one can gain some insight into the complexity contained within *Cancer* sensu lato. The stratigraphic as well as the (paleo)geographic distributions of the species of these genera are fascinating in themselves, but that story is not particularly relevant here. For those who are interested, a study of the papers in the primary literature would prove instructive.

Despite this taxonomic progress, many researchers, especially those not directly involved in taxonomy, still continue to use *Cancer* as a kind of catch-all. Sometimes, the species being so treated are simply not well understood at all. For example, *Cancer setosus* Molina, 1782, is a fairly common South American cancrid often used in physiological and ecological studies. However, as a taxonomic concept, *C. setosus* is rather fuzzy. Molina (1782: 347) described the species from Chile in just two lines, noting that the carapace was setose with tubercles and the frontal margin was bifid and deflexed downwards. No figure was attached and nothing else was said! However, this brevity is common with species described in the very early literature. The relative antiquity of this work also means finding the types will be difficult, if it is even still extant. Subsequently, Poeppig (1836), also working on collections from Chile recognized and described *Cancer polyodon*, but this time, in much greater detail and with a figure, leaving no doubt what the species is. Poeppig even realised that his new species was likely to be the *Cancer setosus* of Molina when he listed this name next to his with a question mark and discussed it (Poeppig, 1836: 133, 134). When Rathbun (1930) reviewed the genus, she could not decide what to do with *C. setosus* and placed it as a junior synonym under *C. polyodon*, a name that was already in wider use; even though Molina's name actually has priority over Poeppig's name. Yet, the name *C. setosus* is still generally employed in Chile. To have two names competing for use side-by-side in the literature is bad enough, that the species itself is now not even a *Cancer* but classified at present in the genus *Romaleon* (cf. Schweitzer and Feldmann, 2000) just adds to the confusion. In this particular case, some clinical, perhaps even "surgical" taxonomic actions and decisions will need to be taken to fix the name once and for all.

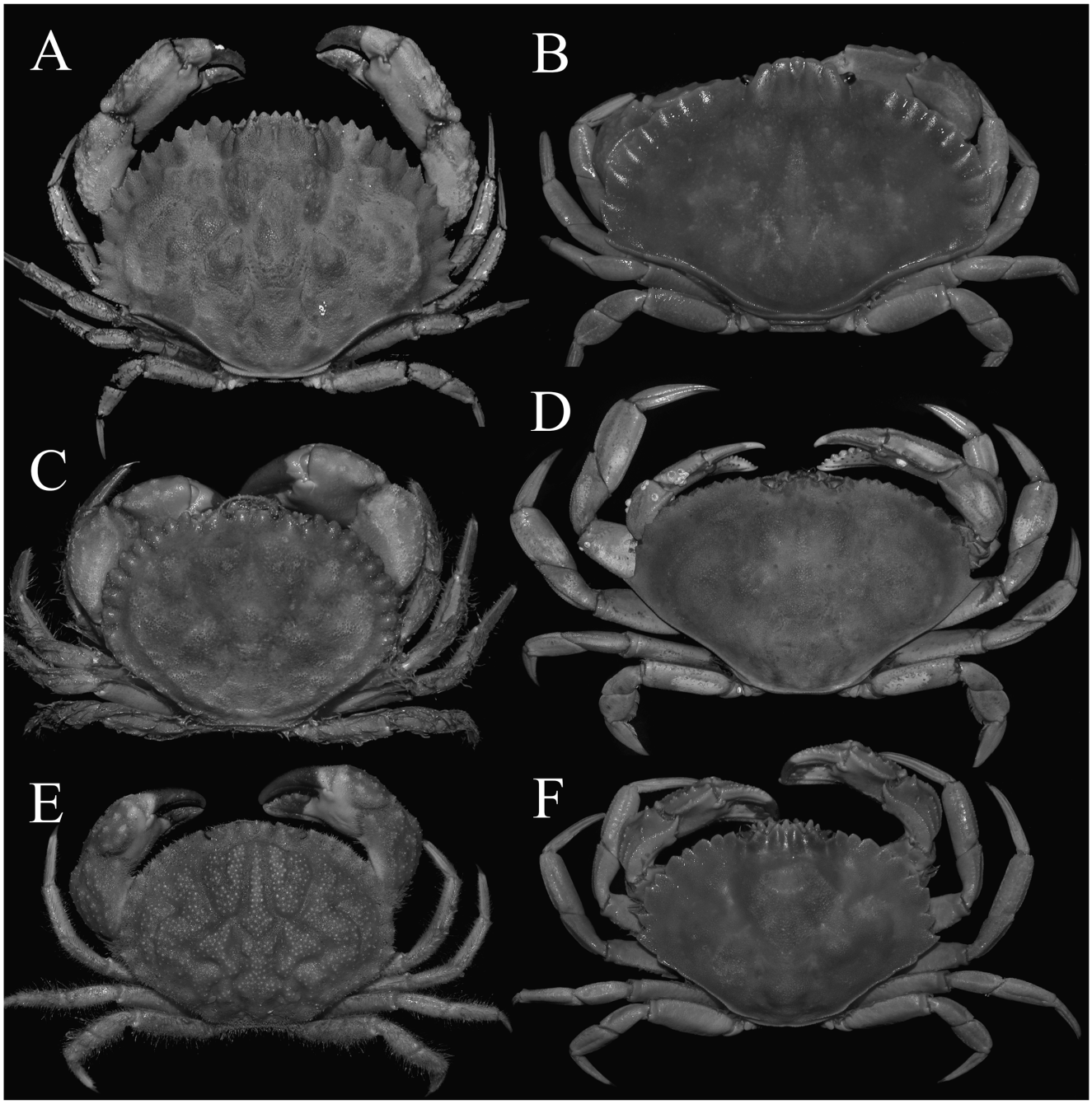
And there is yet another *Cancer* name that has been forgotten since Rathbun (1930: 179) – *Cancer amoenus* Herbst, 1799. No author working on *Cancer* has referred to this name since Rathbun, probably because she regarded it as "indeterminable." Nevertheless, Herbst's name is available. He provided a detailed description and even a figure. Yet his name has been forgotten and the identity of the species unresolved for two centuries. There are also no types (see Sakai, 1999). Fortunately, this problem is easy to solve. His description and figure leaves little doubt that it is what is today known as *Atelecyclus undecimdentatus* (Herbst, 1783) (Atelecyclidae) (Low and Ng, in preparation).

Heart of the Problem

Although taxonomy is a dynamic science, we biologists must strive to use current valid names. Personal whim or individual preference is not a basis for sound science. Some years ago, while editing a volume on barnacle biology, one of the included authors objected to FRS's copy-editing, wherein the generic designation had been updated for one of the species referred to in the paper. The author insisted that if the use of the genus name *Balanus* for the species in question was good enough for Darwin, it was good enough for him; he rejected out of hand the results of a major revision of the balanids published some years before. FRS asked this author for his specific argumentation against the problematic revision, and he claimed the facts were all in Darwin back in the 1850s – he ended up withdrawing his paper from the volume. Dogmatism cannot be the basis for good science. Classifications are hypotheses, which can be accepted as they have been presented, or refuted, if the data is grey. But they must be discussed – it is unscientific (and certainly ungentlemanly) to outright ignore or dismiss published accounts because of personal convenience or beliefs.

Cancrids are, and will continue to be, important species for the study of crustacean physiology, behavior, ecology, reproductive biology, as well as phylogeny. Not to be properly aware of *what something is* risks negating an entire research program. Many years ago, while FRS was at the San Diego Museum, the carcinology staff had to deal with a large jug of preserved specimens of American ghost shrimp that was submitted to the marine invertebrates department "to get a proper name for use in the publication." The material had been collected in connection with long-term physiological study on respiration rates. The paper was being prepared; the authors needed to be sure they had the correct name of what

Fig. 1. Overall views. A, *Anatolikos japonicus* (Ortmann, 1893), male (93.5 × 59.0 mm) (ZRC 2000.7), Ilan, Taiwan; B, *Cancer productus* Randall, 1840, male (41.2 × 27.3 mm) (ZRC 2010.123), Oregon, U.S.A.; C, *Glebocarcinus oregonensis* (Dana, 1852), male (33.7 × 25.3 mm) (ZRC 2002.377), Washington State, U.S.A.; D, *Metacarcinus magister* (Dana, 1852), male (178.2 × 111.0 mm) (ZRC 2002.369), Washington State, U.S.A.; E, *Platepistoma macrophthalmus* Rathbun, 1906, male (48.5 × 37.0 mm) (ZRC 2000.517), Oahu, Hawaii; F, *Romaleon gibbosulum* (De Haan, 1833), male (50.8 × 36.3 mm) (ZRC 2008.126), Yellow Sea, China; G, *Anisospinos berglundi* Schweitzer and Feldmann, 2000 (after Schweitzer and Feldmann, 2000: Fig. 3); H, *Notocarcinus sulcatus* Schweitzer and Feldmann, 2000 (after Schweitzer and Feldmann, 2000: Fig. 8).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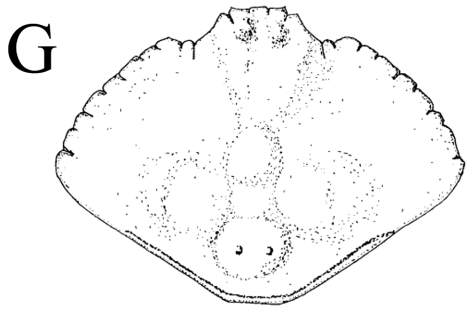
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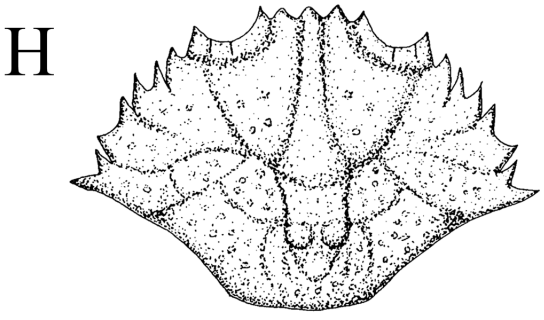
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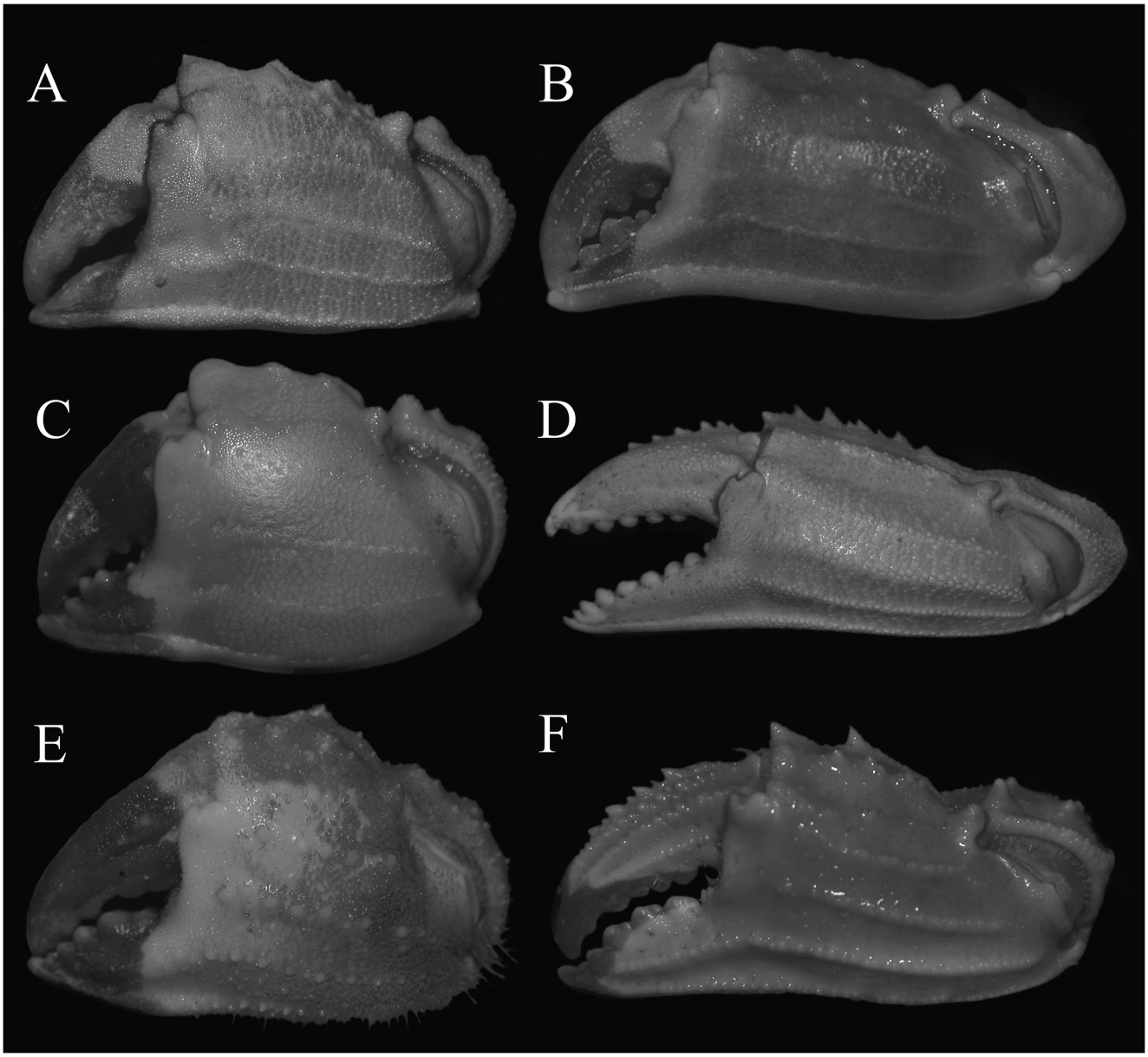
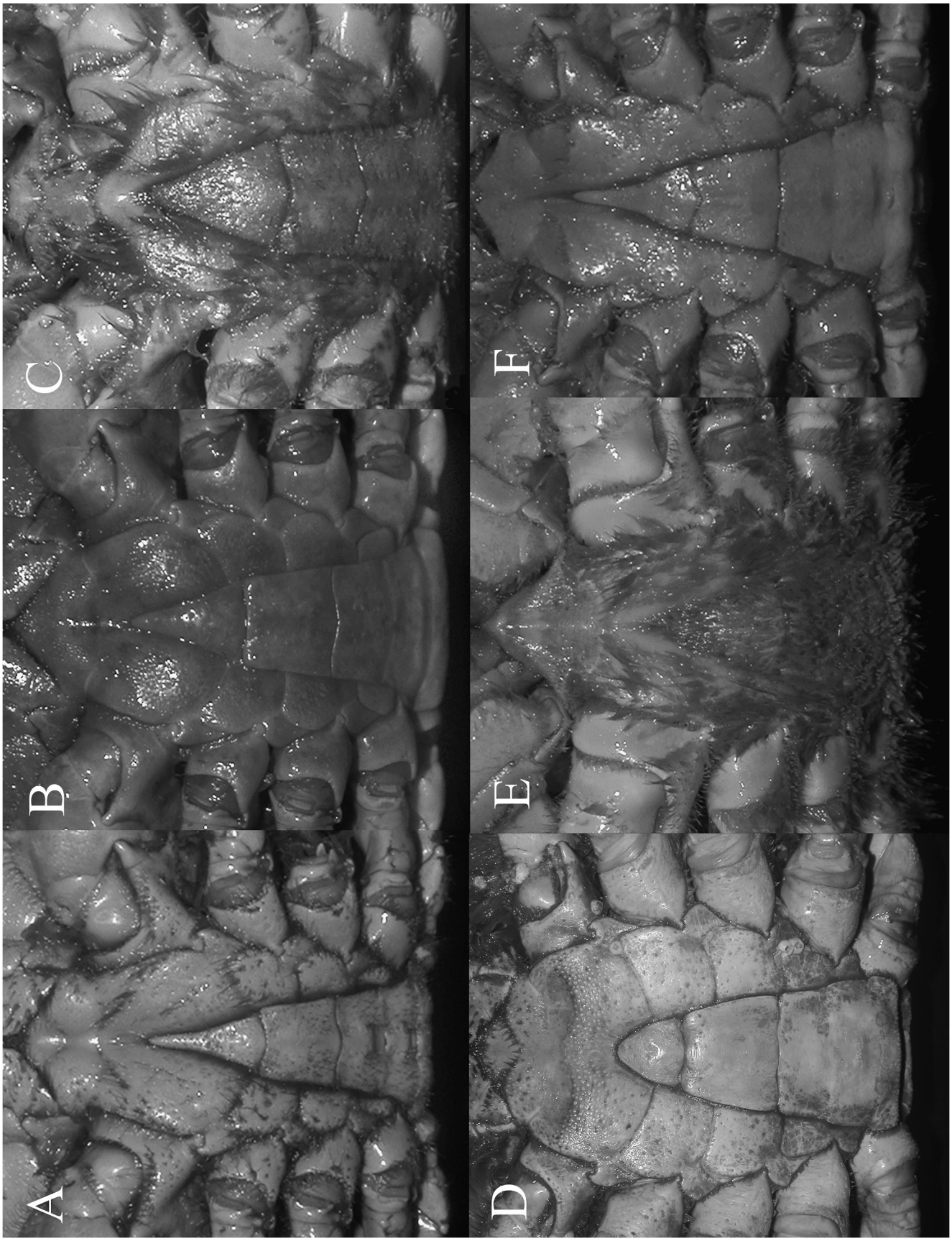


Fig. 2. Outer views of chelae. A, *Anatolikos japonicus* (Ortmann, 1893), male (93.5 × 59.0 mm) (ZRC 2000.7), Ilan, Taiwan; B, *Cancer productus* Randall, 1840, male (41.2 × 27.3 mm) (ZRC 2010.123), Oregon, U.S.A.; C, *Glebocarcinus oregonensis* (Dana, 1852), male (33.7 × 25.3 mm) (ZRC 2002.377), Washington State, U.S.A.; D, *Metacarcinus magister* (Dana, 1852), male (178.2 × 111.0 mm) (ZRC 2002.369), Washington State, U.S.A. [chelae laterally inverted]; E, *Platepistoma macrophthalmus* Rathbun, 1906, male (48.5 × 37.0 mm) (ZRC 2000.517), Oahu, Hawaii; F, *Romaleon gibbosulum* (De Haan, 1833), male (50.8 × 36.3 mm) (ZRC 2008.126), Yellow Sea, China.

they had been working on. The problem became hopeless when examination of the specimens in the jug proved to include several species in at least three genera, plus another taxon that appeared to represent a genus new to science. The entire project had to be aborted. On another occasion, acting as the editor, PKLN accepted and published a paper that revised the commercially important Asian portunid genus *Scylla* De Haan, 1833, which hithero was believed to contain just one species. Keenan et al. (1998) recognised four, and several Asian fisheries researchers lamblasted us for publishing this "terrible" paper and as a result, causing turmoil and making a mockery of their years of hard work. The problem? What they presumed was one species was two, three or even four species – and all their hypothesis

Fig. 3. Male anterior thoracic sterna and pleons. A, *Anatolikos japonicus* (Ortmann, 1893), male (93.5 × 59.0 mm) (ZRC 2000.7), Ilan, Taiwan; B, *Cancer productus* Randall, 1840, male (41.2 × 27.3 mm) (ZRC 2010.123), Oregon, U.S.A.; C, *Glebocarcinus oregonensis* (Dana, 1852), male (33.7 × 25.3 mm) (ZRC 2002.377), Washington State, U.S.A.; D, *Metacarcinus magister* (Dana, 1852), male (178.2 × 111.0 mm) (ZRC 2002.369), Washington State, U.S.A.; E, *Platepistoma macrophthalmus* Rathbun, 1906, male (48.5 × 37.0 mm) (ZRC 2000.517), Oahu, Hawaii; F, *Romaleon gibbosulum* (De Haan, 1833), male (50.8 × 36.3 mm) (ZRC 2008.126), Yellow Sea, China.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and findings have become dubious – perhaps even wrong – because they had analysed multiple species data sets as if they were one! Should science be ignored or even submerged because it is an "inconvenient truth"? Never. And in the years since 1998, the bulk of research papers have vindicated the "incovenient" conclusions of Keenan et al.

These are only two examples of how efforts of taxonomists are often not taken seriously. Why this is so could be due to several issues, but undoubtedly one is the near invisibility of taxonomy as a science. The use of a binomen in a paper rarely gets a proper citation either in the text, or in the References at the end of a paper. As a result, advances are made in understanding species and pass completely by the notice of researchers in fields such as ecology, behaviour, and physiology – disciplines that obtain their legitimacy, whether they realize it or not, from the proper use of nomenclature.

SYSTEMATICS

Hence, for the sake of proper references to species of cancrids in future issues of this journal, as well as other places in the scientific literature, please consider this listing of currently accepted species of living cancrids (Ng et al., 2008). For those interested in the extensive array of fossil cancrids, they should consult Schweitzer and Feldmann (2000) (see also De Grave et al., 2009). We also note that while the current hypotheses for the generic classification of Cancridae appear to be reasonably sound on the basis of the available morphological data, it is by no means universally accepted nor is it the last word. There are still aspects of cancrid taxonomy that require more detailed study, and this, together with the discovery of more and better fossils, may change the classification. In addition, the preliminary DNA data (Harrison and Crespi, 1999) also does not appear to support the classification, although things may change with the rapidly developing technology and molecular phylogenetic methods. That been said, the classification proposed by Schweitzer and Feldmann (2000) remains the most parsimonious system available, and detractors who feel that recognising only one genus, *Cancer*, is preferable, must make the case why a multi-generic system is unusable.

Checklist of Living Cancridae

Cancridae Latreille, 1802
- Cancerides Latreille, 1802
- Trichoceridae Dana, 1852

Cancrinae Latreille, 1802

Anatolikos Schweitzer and Feldmann, 2000 (type species, *Cancer japonicus* Ortmann, 1893)
- *A. japonicus* (Ortmann, 1893) [*Cancer*]
  - = ?*Cancer sanbonugii* Imaizumi, 1962
  - = ?*Cancer odosensis* Imaizumi, 1962
  - = ?*Cancer imamurae* Imaizumi, 1962
- *A. tumifrons* (Yokoya, 1933) [*Cancer*]

Cancer Linnaeus, 1758 (type species *Cancer pagurus* Linnaeus, 1758)
- = *Platycarcinus* H. Milne Edwards, 1834 (type species *Cancer pagurus* Linnaeus, 1758, subsequent designation by Rathbun, 1930; gender masculine)
- *C. bellianus* Johnson, 1861
- *C. borealis* Stimpson, 1859
- *C. irroratus* Say, 1817
- *C. johngarthi* Carvacho, 1989
- *C. pagurus* Linnaeus, 1758 [Direction 36]
  - = *C. luederwaldti* Rathbun, 1930
- *C. plebejus* Poeppig, 1836
  - = ?*C. coronatus* Molina, 1782
  - = *C. irroratus* Bell, 1835 (pre-occupied name)
- *C. porteri* Rathbun, 1930
  - = *C. longipes* Bell, 1835 (pre-occupied name)
- *C. productus* Randall, 1840
  - = *C. perlatus* Stimpson, 1856
  - = *C. breweri* Gabb, 1869

Glebocarcinus Nations, 1975
- = *Glebocarcinus* Nations, 1975 (type species *Trichocera oregonensis* Dana, 1852)
- *G. amphioetus* (Rathbun, 1898) [*Cancer*]
  - = *Trichocarcinus dentatus* Miers, 1879 (pre-occupied name)
  - = *C. pygmaeus* Ortmann, 1893 (pre-occupied name)
  - = *C. bullatus* Balss, 1922
- *G. oregonensis* (Dana, 1852) [*Trichocera*]
  - = *Platycarcinus recurvidens* Bate, 1864
  - = *Trichocarcinus walkeri* Holmes, 1900
  - = *Lophopanopeus somaterianus* Rathbun, 1930

Metacarcinus A. Milne-Edwards, 1862 (type species *Cancer magister* Dana, 1852)
- *M. anthonyi* (Rathbun, 1897) [*Cancer*]
- *M. edwardsii* (Bell, 1835) [*Cancer*]
  - = *C. edwardsii* var. *annulipes* Miers, 1881
- *M. gracilis* (Dana, 1852) [*Cancer*]
- *M. magister* (Dana, 1852) [*Cancer*]
- *M. novaezelandiae* (Hombron and Jacquinot, 1846) [*Platycarcinus*]

Platepistoma Rathbun, 1906 (type species *Platepistoma macrophthalmus* Rathbun, 1906)
- *P. anaglyptum* (Balss, 1922) [*Cancer*]
  - = *C. sakaii* Takeda and Miyake, 1972 (unnecessary replacement name for *C. anaglyptus* Balss, 1922)
  - = *C. margaritarius* Crosnier, 1976
- *P. balssii* (Zarenkov, 1990) [*Cancer*]
- *P. guezei* (Crosnier, 1976) [*Cancer*]
- *P. kiribatiense* Davie, 1991
- *P. macrophthalmus* Rathbun, 1906
- *P. nanum* Davie, 1991
- *P. seychellense* Davie, 1991

Romaleon Gistel, 1848
- = *Corystes* (*Trichocera*) De Haan, 1833 (type species *Corystes* (*Trichocera*) *gibbosula* De Haan, 1833, by monotypy; name pre-occupied by *Trichocera* Meigen, 1803 [Diptera]; gender feminine)
- = *Romaleon* Gistel, 1848 (replacement name for *Corystes* (*Trichocera*) De Haan, 1833; gender neuter)
- = *Trichocarcinus* Miers, 1879 (replacement name for *Cancer* (*Trichocera*) De Haan, 1833; gender masculine)
- *R. antennarium* (Stimpson, 1856) [*Cancer*]
- *R. branneri* (Rathbun, 1926) [*Cancer*]
- *R. gibbosulum* (De Haan, 1833) [*Corystes* (*Trichocera*)]
  - = *Trichocarcinus affinis* Miers, 1879
- *R. jordani* (Rathbun, 1900) [*Cancer*]
- *R. luzonense* (Sakai, 1983) [*Cancer*]

R. nadaense (Sakai, 1969) [*Cancer*]
R. polyodon (Poeppig, 1836) [*Cancer*]
= ?*C. setosus* Molina, 1782
= *C. dentatus* Bell, 1835

Incertae sedis
Trichocera porcellana Adams and White, 1849

Key to Genera of Cancrinae

To facilitate identification at least to genus of new material, we have substantially modified the key in Schweitzer and Feldmann (2000) for the various cancrine genera. While thoracic sternal and chelal characters are not available for the two fossil genera, they are figured for the extant genera (Figs. 1-3) to aid in their identification as there are some indicative features present, e.g., the distinctive rounded male telson of *Metacarcinus* (Fig. 2D).

1a. Carapace with even number of frontal spines; posterolateral margin with numerous coarse granules or spines . . . . . †Lobocarcininae
1b. Carapace with odd number of frontal spines; posterolateral margin smooth or with one or two small spines . . . . . Cancrinae [2]
2a. Carapace appears rounded, not much wider than long; carapace surface with regions well demarcated by deep grooves or with strong granulose ornaments; carapace margins and pereiopods prominently setose, often obscuring margins and/or surfaces (Figs. 1C, E; 3C, E) 3
2b. Carapace much wider than long; carapace regions weakly demarcated or not distinct; never densely covered with granules or large ornaments; carapace margins and pereiopods with scattered setae, never obscuring margins and/or surfaces (Figs. 1A, B, D, F; 3A, B, D, F) 4
3a. Dorsal carapace surface with well-defined, evenly granulated and setose regions separated by deep, prominent grooves (Figs. 1E, 3E); outer surface of chela setose (Fig. 2E); deep-sea taxa . . . . . *Platepistoma*
3b. Dorsal carapace surface with regions poorly demarcated, without prominent grooves or setae, but may have large granular patches and ornaments (Figs. 1C, 3C); outer surface of chela setose (Fig. 2C); shallow-water species . . . . . *Glebocarcinus*
4a. Posterolateral margin with distinct tooth or tubercle on anterior third (Fig. 1A, F) 5
4b. Posterolateral margin unarmed (Fig. 1B-E) 7
5a. Most of anterolateral teeth/spines distinctly arranged in pairs, separated by deep clefts (Fig. 1H) . . . . . †*Anisospinos*
5b. Anterolateral spines/teeth single or vaguely grouped in pairs, separated by clefts or fissures (Fig. 1A, B, D, F) 6
6a. Dorsal carapace surface relatively smooth, regions poorly demarcated; anterior anterolateral teeth separated by fissures (Fig. 1F), posterior ones seprated by prominent clefts; adult chelae relatively elongate (Fig. 2F) . . . . . *Romaleon*
6b. Dorsal carapace surface with regions demarcated by patches of granules smooth, grooves separating them indistinct (Fig. 1A); all anterolateral teeth separated by prominent fissures, some appearing paired because of alternating deeper fissures; adult chelae relatively short (Fig. 2A) . . . . . *Anatolikos*
7a. Anterolateral teeth distinct, sharp, may be spiniform; separated by short fissures or clefts or differing degrees (Fig. 1D) . . . . . *Metacarcinus*
7b. Anterolateral teeth relatively low, lobiform, separated by deep fissures (Fig. 1B) 8
8a. Epigastric and hepatic regions gently concave to almost flat (Fig 1B) . . . . . *Cancer*
8b. Epigastric and hepatic regions prominently concave, appears depressed (Fig. 1G) . . . . . †*Notocarcinus*

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