

ANNOTATED CHECKLIST OF ANOMURAN DECAPOD CRUSTACEANS OF THE WORLD (EXCLUSIVE OF THE KIWAOIDEA AND FAMILIES CHIROSTYLIDAE AND GALATHEIDAE OF THE GALATHEOIDEA) – PREAMBLE AND SCOPE

Patsy A. McLaughlin

Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-4042, USA
Email: hermit@fidalgo.net

Christopher B. Boyko

Department of Biology, Dowling College, 150 Idle Hour Blvd., Oakdale, NY 11769, USA
Email: cboyko@amnh.org

Keith A. Crandall

Department of Biology and Monte L. Bean Life Science Museum
401 Widtsoe Building, Brigham Young University, Provo, UT 84602, USA
Email: keith.crandall@byu.edu

Tomoyuki Komai

Natural History Museum and Institute, Chiba, 955-2 Aoba-cho, Chuo-ku, Chiba, 260-8682 Japan.
Email: komai@chiba-muse.or.jp

Rafael Lemaitre

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution,
4210 Silver Hill Road, Suitland, Maryland 20746, USA
Email: lemaitrr@si.edu

Masayuki Osawa

Research Center for Coastal Lagoon and Environments, Shimane University,
1060 Nishikawatsu-cho, Matsue, Shimane 690-8504, Japan
Email: osawam@soc.shimane-u.ac.jp

Dwi Listyo Rahayu

UPT Mataram, Indonesian Institute of Sciences (LIPI), Teluk Kodek, Pemenang, Lombok Barat 83352, NTB, Indonesia
Email: dwilistyo@yahoo.com

ABSTRACT. – Annotated checklists of the world’s Recent anomuran crustacean superfamilies Aegloidea, Hippoidea, Lithodoidea, Lomisoidea, Paguroidea and galatheoid family Porcellanidae are presented. Each is accompanied by brief reviews of the historical aspects of its classification, general external morphology, features of larval development and current phylogenetic status. This presentation is divided into four parts because the only unifying threads among the Aegloidea, Hippoidea, Porcellanidae and the crab-like Lithodoidea and Lomisoidea are their shared anomuran apomorphies and mutually exhibited, but independently evolved, carcinization. That carcinization similarly links the latter two superfamilies with the Paguroidea is still a passionately debated matter that will be briefly addressed, but certainly not resolved. The checklists include all currently recognized valid species, primary synonyms and homonyms, notes on matters of confusion and/or misunderstanding, and complete bibliographic references to all original descriptions. The lists are enhanced by a collection of photographs depicting the variety exhibited by members of these taxa.

KEY WORDS. – Checklists, valid taxa, primary synonyms, homonyms.

PREAMBLE

While the Brachyura Linnaeus, 1758 may claim the highest degree of diversity seen among decapod crustaceans (Ng et al., 2008), the Anomura certainly exhibits the greatest disparity within the Order Decapoda Latreille, 1802 despite being adjudged a monophyletic infraorder by both morphological and molecular studies (Scholtz & Richter,

1995; Schram, 2001; Dixon et al., 2003; Ah Yong & O’Meally, 2004; Porter et al., 2005; McLaughlin et al., 2007; Ah Yong et al., 2009; Bracken et al., 2009). Their evolutionary novelties notwithstanding, anomurans often have been united through the process of carcinization — the development of a crab-like body form. As originally hypothesized by Borradaile (1916), carcinization was not perceived as the process by which a hermit crab abandoned its gastropod carcinoecium and was

transformed into a free-living lithodid crab, although that is the interpretation that has evolved. Borradaile's focus was on the unusual and atypical hermit crab genus *Porcellanopagurus* Filhol, 1883, and he considered its crab-like appearance quite independent of carcinization in other anomurans. Borradaile (1916) interpreted the widening of the sternite of its third maxillipeds as the first step in carcinization. Further advances included broadening of the cephalothorax and accompanying calcification. He gave only passing attention to reduction and carriage of the pleon, a principal element in the current definition of carcinization.

Although the restrictive "hermit to king" hypothesis still prevails in many analyses, there also is morphological and molecular evidence to support the belief that carcinization evolved independently in more than one major anomuran taxon (e.g., Sternberg, 1996; McLaughlin & Lemaitre, 1997; Morrison et al., 2002). However, a detailed discussion of carcinization is not appropriate for these checklists. Suffice it to say that while members of all of these major taxa exhibit certain attributes of the phenomenon of carcinization, each is provided with morphological characters that set it apart from the others, and all in turn are set apart from the Brachyura by the synapomorphies of Anomura listed below.

In general terms, the Anomura are best described as having an assortment of adult body shapes from lobster-like to true crab-like. About the only universally shared characters are the marked reduction of fifth pereopods that are not used as ambulatory appendages, the articulated or missing eighth thoracic sternite and the cephalothorax that is not fused to the epistome as it is in brachyurans. The reduction of the fifth pereopods, however, is not exclusively an anomuran character; it also is seen in the basal Brachyura. The anomuran cephalothorax may be weakly to well calcified and the carapacial coverings varying in extent, shape and ornamentation. The anomuran pleon exhibits similar plasticity, from moderately well calcified with clearly identifiable pleura to membranous with little if any visible evidence of segmentation. The pleon may be carried posteriorly, twisted to accommodate an external covering such as a gastropod shell, or tightly tucked under the cephalothorax. Like brachyurans, anomurans occupy a broad spectrum of habitats from terrestrial atolls to abyssal seas and while the majority of species are marine, some also have colonized terrestrial and freshwater environments.

Classifications of this major group of decapods, like the hierarchical names themselves and their authorships, have been controversial. McLaughlin & Holthuis (1985) reviewed the histories and applications of both *Anomala* Latreille, 1817 and *Anomura* MacLeay, 1838, and concluded that as rules of nomenclature did not apply above the family level, the junior name *Anomura*, which had more common usage, should be adopted for those decapods represented by the Galatheaidea Samouelle, 1819, Hippoidea Latreille, 1825, Lomisoidea Bouvier, 1895 (as Lomoidea) and Paguroidea Latreille, 1802. And while, with few exceptions, the *Anomura* (or *Anomala*) always has been comprised of the hippids, galatheids and pagurids, in the past, for one author or another

it also has included, or excluded, the porcellanids, lithodids, thalassinids, *Lomis* H. Milne Edwards, 1837, dromiids, homolids and raninids. Numerous authors, including McLaughlin (1980) and Bowman & Abele (1982) incorrectly credited authorship of the *Anomura* to H. Milne Edwards (1832). With the acceptance by Martin & Davis (2001) of *Anomura* in their "Updated Classification of the Recent Crustacea" this infraordinal name has increasingly gained favorable reception and its correct authorship recognized. In these checklists, while we concur with Martin & Davis in the use of *Anomura*, we have adopted the classification of McLaughlin, et al. (2007) for the family group taxa, as did De Grave et al. (2009).

SCOPE

With the exceptions the superfamily Kiwaoidea and families Chirostylidae and Galatheaidea of the superfamily Galatheaidea, treated elsewhere (Baba et al., 2008), annotated checklists of the Recent anomuran crustacean superfamilies of the world, are presented. These checklists are limited to the currently recognized valid taxa in each superfamily or family; the format utilized follows that of Ng et al.'s (2008) *Systema Brachyurorum: Part I*. Each major taxon is introduced with brief summaries of its morphological attributes, larval development and current phylogenetic status. At the family group level, we have provided what we believe to be complete lists of synonyms. At the genus group level, we have provided the current valid names together with their primary synonyms, type species and gender. At the species group level, the currently accepted binomials are given as well as primary synonyms and homonyms, and any misspelling that we are aware of. When generic names have changed, the original genus is indicated in square brackets, following the entry, but no attempt has been made to trace all generic transfers, misidentifications and/or misinterpretations by subsequent investigators. For each of the entries, the original reference is given in the Literature Cited. If a name is preoccupied by a senior homonym, the senior name and its reference also are given. For each family, a series of notes is provided to clarify points of confusion and/or misunderstanding. These are indicated by bracketed { } numbers following the specific taxa that correspond to the same numbers in the Notes section for that family.

ACKNOWLEDGEMENTS

The authors of the aegloid checklist express their deep gratitude to Dr. Georgina Bond-Buckup for her review and updating of the checklist for that superfamily. One of the authors (KAC) acknowledges U.S. National Science Foundation grant NSF EF-0531762 and the Biodiversity Synthesis Center for stimulating thought of the production of checklists for decapod crustaceans. One of the photo contributors (DLF) acknowledge U.S. National Science Foundation grants BS&I DEB-0315995 and ATOL EF 0531603 as well as logistic support of Smithsonian Institution laboratories and colleagues in Florida, Belize and Panama.

The value of the present checklists has been appreciably enhanced by the many accompanying photographs, for which we are most grateful to the numerous colleagues who provided us with their talented efforts. The design and layout are the work of Dr. R. Lemaitre. Special thanks are due Dr. Peter K. L. Ng for awakening our interest in compiling these data on the Anomura and making the media outlet available. The Raffles Bulletin staff, particularly Dr. Swee Hee Tan, provided the editorial guidance needed to prepare the manuscript for publication. Rose A. Gullede was of invaluable assistance in the preparation of the photographic plates and in resolving some of the problems with the literature citations. George Holm provided the translations from Danish. Photo contributors are listed here in alphabetical order and individual credits appear in the legend for each photo. Unless otherwise indicated, color photographs were taken of specimens as fresh as possible.

A. Anker	C. Lukhaup
P. Bacchet	M. Marmach
C. B. Boyko	J. W. Martin
T. -Y. Chan	M. Mitsugi
R. Cléva	S. Ohta
K. A. Crandall	M. Osawa
J. -F. Dejouannet	G. Paulay
D. L. Felder	J. Poupin
D. Fenolio	T. Smit
O. Gargominy	H. Tachikawa
G. Jensen	S. Thurston
T. Komai	C. d'Udekem d'Acoz
R. Lemaitre	

LITERATURE CITED

- Ahyong, S. T. & D. O'Meally, 2004. Phylogeny of the Decapoda Reptantia: Resolution using three molecular loci and morphology. *Raffles Bulletin of Zoology*, **52**: 673–693.
- Ahyong, S. T., K. E. Schnabel & E. W. Maas, 2009. Anomuran Phylogeny: New insights from molecular data. In: Martin, J. W., K. A. Crandall & D. L. Felder (eds.), *Decapod Crustacean Phylogenetics. Crustacean Issues 18*. CRC Press, Boca Raton, FL, New York, London. Pp. 399–414.
- Baba, K., E. Macpherson, G. C. B. Poore, S. T. Ahyong, A. Bermudez, P. Cabezas, C.-W. Lin, M. Nizinski, C. Rodrigues & K. E. Schnabel, 2008. Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura—families Chirostylidae, Galatheididae and Kiwaidae). *Zootaxa*, **1905**: 1–220.
- Borradaile, L. A., 1916. Crustacea. Part II. *Porcellanopagurus*: An instance of carcinization. In: *British Antarctic ("Terra Nova") Expedition, 1910. Natural history report. Zoology*, **3**(3): 111–126.
- Bouvier, E.-L., 1895. Recherches sur les affinités des *Lithodes* & des *Lomis* avec les Pagurides. *Annales des Sciences Naturelles, Zoologie et Paléontologie*, (7)**18**:157–213.
- Bowman, T. E. & L. G. Abele, 1982. Classification of the Recent Crustacea. In: *The Biology of Crustacea*. 1. *Systematics, the fossil record and biogeography*. Abele, L. G. (ed.), Academic Press, New York. Pp. 1–27.
- Bracken, H. D., A. Toon, D. L. Felder, J. W. Martin, M. Finley, J. Rassmussen, F. Palero & K. A. Crandall, 2009. The decapod Tree of Life: Compiling the data and moving toward a consensus of decapod evolution. *Arthropod Systematics and Phylogeny*, **67**(1): 99–116.
- De Grave, S., N. D. Pentcheff, S. T. Ahyong, T.-Y. Chan, K. A. Crandall, P. C. Dworschak, D. L. Felder, R. M. Feldmann, C. H. J. M. Franssen, L. Y. D. Goulding, R. Lemaitre, M. E. Y. Low, J. W. Martin, P. K. L. Ng, C. E. Schweitzer, S. H. Tan, D. Tshudy & R. Wetzer, 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology, Supplement 21*: 1–109.
- Dixon, C. J., S. T. Ahyong & F. R. Schram, 2003. A new hypothesis of decapod phylogeny. *Crustaceana*, **76**: 935–975.
- Latreille, P. A., 1802. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*, Vol. 3. Paris. 467 pp.
- Latreille P. A., 1817. Macroures, Macrourea. *Nouveau Dictionnaire d'Histoire naturelle*, **18**: 357–358.
- Latreille, P. A., 1825. *Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres*. J.-B. Baillière, Paris. 570 pp.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis locis*, (edition 10) 1: 1–824. Holmiae.
- Martin, J. W. & G. E. Davis, 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science, Series 39*: 1–124.
- MacLeay, W. S., 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith, A., *Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa"*. Smith, Elder, and Co., London. Pp. 53–71.
- McLaughlin, P. A., 1980. *Comparative Morphology of Recent Crustacea*. W. H. Freeman & Company, San Francisco, CA. 177 pp.
- McLaughlin, P. A. & L. B. Holthuis, 1985. Anomura versus Anomala. *Crustaceana*, **49**(2): 204–209.
- McLaughlin, P. A. & R. Lemaitre, 1997. Carcinization -- fact or fiction? I. Evidence from adult morphology. *Contributions to Zoology, Amsterdam*, **67**(2): 79–123.
- Milne Edwards, H., 1832. Recherches sur l'organisation et la classification naturelle des Crustacés Décapodes. *Annales des Sciences Naturelles Zoologie, Paris*, **25**: 298–332.
- Milne Edwards, H., 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. 2: 1–532; atlas, pp. 1–32, pls. 1–42. Librairie Encyclopédique de Roret, Paris.
- Morrison, C. L., A. W. Harvey, S. Lavery, K. Tieu, Y. Huang & C. W. Cunningham, 2002. Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like body form. *Proceedings of the Royal Society, London*, **269**: 345–350.
- Ng, P. K. L., D. Guinot & P. J. F. Davie, 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology, Supplement 17*: 1–286.
- Porter, M. L., M. Perez-Losada & K. A. Crandall, 2005. Model based multi-locus estimation of decapod phylogeny and divergence times. *Molecular Phylogenetics and Evolution*, **37**: 355–369.

- Scholtz, G. & S. Richter, 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society*, **113**: 289–328.
- Schram, F. R., 2001. Phylogeny of decapods: moving towards a consensus. *Hydrobiologia*, **449**: 1–20.
- Samouelle, G., 1819. *The entomologist's useful compendium; or an introduction to the knowledge of British insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and the modern method of arranging the classes Crustacea, Myriapoda, Spiders, Mites and Insects, from their affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance and usual situations of near 3,000 species of British insects; with instructions for collecting and fitting up objects for the microscope.* London. 496 pp.
- Sternberg, R. von, 1996. Carcinization as an underlying synapomorphy for the decapod crustacean taxon Meiura. *Evolutionary Theory*, **11**: 153–162.