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THE FIRST 30 YEARS OF THE JOURNAL OF CRUSTACEAN BIOLOGY – SYSTEMATICS AND EVOLUTION

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ABSTRACT

Papers within the broad designation of systematics have figured prominently in the pages of the Journal of Crustacean Biology in its first 30 years. The journal has had great continuity in its editorial policies and practices, having had only three General Editors in 30 years. Not only has the journal published taxonomic material, but also made available material in a variety of subjects that impinge on understanding the evolution and phylogeny of crustaceans, including cladistic phylogeny, biogeography, comparative anatomy, and issues of natural history. An overview of some highlights from the first 30 volumes of the journal is presented; some prognostications for the future are offered.

KEY WORDS: systematics overview

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INTRODUCTION

Articles concerning systematics, phylogeny, biogeography, comparative anatomy, and issues of natural history have held an important place in the pages of the Journal of Crustacean Biology (JCB) right from the very beginning, in fact quite literally (Schram, 1981). I had nothing to do with attaining that most honorable position of "volume 1, number 1, page 1" bestowed on me by our first editor, Arthur Humes, although that manuscript may have been among the first to be submitted. I had originally intended to publish that particular article as part of the proceedings of the Second Crustacean Conference held at the Australian Museum in Sydney in 1980. However, when publication of that volume was delayed, I pulled the paper [the impatience of youth] and submitted it to the then-new JCB. That first JCB paper reviewed matters of eumalacostracan classification, albeit in what I came to realize was more of a phenetic analysis rather than cladistic. The paper contained the creation of a number of new high taxonomic categories within Eumalacostraca, not all of them having withstood the test of time; be that as it may, I believe the paper did trigger a wide ranging discussion and assessment of the classification and evolution of malacostracans that is still going on today (cf. Regier et al., 2010; Koenemann et al., 2010). As for phenetic analysis of arthropod form, the work of Wills et al. (1997) did a far more effective job than my effort.

That first volume of JCB had a number of notable systematic papers, including the following highlights: a supposed record of the remnants of compound eyes in cephalocarids (Burnett, 1981; see below); a review of grooming behavior in decapods (Bauer, 1981); an alternative view of peracarid phylogeny (Watling, 1981); a critical paper on the behavior of stomatopods and their evolution (Reaka and Manning, 1981); and the first remipede with erection of the class (Yager, 1981; see below). Taken together with the large number of taxonomic papers in volume 1, the year 1981 was a very good year for crustacean systematics in JCB and helped get the journal off to a good start.

The purpose of this review is to throw some light on the publication of papers in the broad field of systematics in the first 30 years of the JCB. In the following, I look at the pace of alpha-taxonomy descriptions in the first 30 volumes, the significant expansion of our knowledge concerning particular higher taxa we have fostered, outline the "firsts" for JCB, review some of the controversies we have refereed, and point out some overlooked gems in our array of articles.

TAXONOMY

JCB has at times been characterized as a taxonomy journal – this done sometimes in a disparaging way. There is no denying that JCB has published its fair share of alpha-taxonomic descriptions. Figure 1 charts the "ups and downs" of this process. While volume 1 of JCB contains the description of some 31 new species, the number of species descriptions dropped steadily thereafter for a number of years, even within volume 1, with only a single species being described by the time we published issue 4. However, there were some spikes in species descriptions that juggled the absolute numbers within any single year. One such spike occurred in 1986 and was related to a Festschrift issue in honor of Fenner Chace, a specialist in Caridea at the Smithsonian Natural History Museum. The number of patronyms created in Chace's honor took place of prominence in that issue. An even more impressive spike occurred in 2000-2001 with two Festschriften: a special volume in honor of Raymond Manning in 2000, and a memorial issue for our first editor, Arthur Humes, in 2001. Patronyms are part of the tradition in the field of taxonomic biology commemorative volumes, but if we remove from the total count those new species described in these special issues, the production of new species fluctuates nicely around a background mean. I did not do a regression

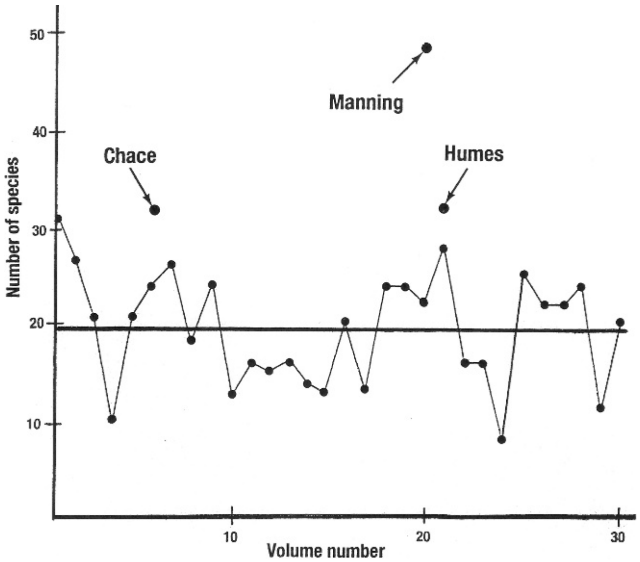

Fig. 1. Pattern of species descriptions through the first 30 volumes of the Journal of Crustacean Biology. The average of 19.6 species per volume denoted by the horizontal line. The especially high peaks connected to the three special Festschrift issues for Fenner Chance (vol. 6), Raymond Manning (vol. 20), and Arthur Humes (vol. 21) indicated by outlying points.

analysis, but I suspect that the slope over the 30 years may be slightly negative, with fewer taxonomic descriptions appearing in recent years.

While it remains true that almost every issue of JCB generally has had at least one new species described within its pages, this has not always been the case. In 1985, volume 5, issue 2, had no new species descriptions (although there was a new genus in that issue). However, we had to wait another 10 years until 1995 in issue 15(1) before that happened again, and that was repeated in 2002 with 22(1). Hence, in retrospect JCB has been no more of a "taxonomic journal" than its sister journals, e.g., Crustaceana, Nauplius, or Crustacean Research. It might be interesting to compare absolute numbers, but such a study is beyond the scope of this paper.

In addition to basic species descriptions (some 606 of them to date), JCB has had a tremendous impact on the higher classification of the crustaceans. Indeed, we have published the erection of 2 classes, 5 orders, 1 suborder, and 7 superfamilies (Table 1 affords an overview of these). In addition, the pages of JCB include recognition of some 40 families, 14 subfamilies, 188 genera, and 5 subgenera.

Clearly, JCB has had a most significant impact on our understanding of crustacean biodiversity.

Group "Monographs"

Of course, if all we were interested in were the production of alpha-taxonomy papers, the editors of JCB would have failed the mission of The Crustacean Society: to foster increase in and dissemination of knowledge of crustaceans. Greater consequence than the alpha-taxonomic descriptions, however, resides in the articles we have published that have significantly impacted our understanding of the biology and natural history of important crustacean groups.

Remipedia.—A cluster of JCB papers dealing with various aspects of the study of the remipedes illustrates the point. Remipede papers began of course with the description of the first species and erection of the class Remipedia (Yager, 1981). After that, other notable remipede articles appeared in JCB. Ito and Schram (1988) determined the basic anatomical arrangements of the reproductive organs and discovered the separate location of the female and male gonopores. The following year, Ito (1989) published an interesting comparative study concerning possible origins of the remipede thoracic limbs, with special references to the appendage segmentation seen in copepods and cephalocarids. Building on Robert Hessler's expertise in crustacean skeleto-musculature, Hessler and Yager (1998) examined that same system in *Speleonectes*.

Of course remipede papers did appear in other places. The original work on the unique form and function of the remipede maxillules (Schram and Lewis, 1989) appeared in Crustacean Issues, but van der Ham and Felgenhauer (2007) carried this line of investigation further along in a detailed study published in JCB that confirmed the hypodermic nature of the maxillule and its associated glands. Koenemann et al. (2007) recorded observations from both laboratory and field studies concerning the behavior of *Speleonectes*.

Table 1. Summary of taxa above the family level erected in the Journal of Crustacean Biology.

Level	Taxon	Reference
Class	Remipedia Yager, 1981	1(3): 328-333
Class	Tantulocarida Boxshall and Lincoln, 1983	3(1): 1-16
Order	Belotelsonidea Schram, 1981	1(1): 1-10
Order	Hemicaridea Schram, 1981	1(1): 1-10
Order	Waterstonellidea Schram, 1981	1(1): 1-10
Order	Mictacea Bowman, Garner, Hessler, Iliffe, and Sanders, 1985	5(1): 74-78
Order	Thaumatopsylloidea Ho, Dojiri, Hendler, and Deets, 2003	23(2): 582-594
Suborder	Scutocoxifera Dryer and Wägele, 2002	22(2): 217-234.
Superfamily	Fosshagenioidea, Suarez-Morales and Iliffe, 1996	16(4): 754-762
Superfamily	Galatheacaridoidea Vereshchaka, 1997	17(2): 361-373
Superfamily	Aetiopedesoidea Myers and Lowry, 2003	23(2): 443-485
Superfamily	Chevalioidea Myers and Lowry, 2003	23(2): 443-485
Superfamily	Microprotopoidea Myers and Lowry, 2003	23(2): 443-485
Superfamily	Rakiroidea Myers and Lowry, 2003	23(2): 443-485
Superfamily	Camponocancroidea Feldmann, Schweitzer, and Green, 2008	28(3): 502-509

JCB also offered several contributions towards increasing our knowledge of remipede biodiversity. Yager (1994) described *S. gironensis* from Cuba; Wollermann et al. (2007) dealt with a new species of the distinctive genus *Cryptocorynetes*, *C. longulus*. Finally, Koenemann et al. (2008), while describing *Pleomothra fragilis*, recognized for the first time remipede larvae.

Tantulocarida.—The other new class that appeared in the early issues of JCB was Tantulocarida Boxshall and Lincoln, 1983. The most intriguing aspect of that recognition to me was the tiny size of the tantulocarids – in that first paper recorded as an ectoparasite on a harpacticoid copepod. The occurrence of tantulocarids on other groups as well has been extended since 1983 (Boxshall, 1996).

The reduced form of the tantulocarid body (not only in size, but also in diagnostic components) stirred great interest as to just what were the higher affinities of the class. Boxshall and Huys (1989) began to fill in the blanks with the description of a new species and the inclusion of a phylogenetic analysis of maxillopodans; this indicated affinities of tantulacarids might be with a clade containing ostracodes, branchiurans, and thecostracans. The crowning achievement, however, arrived when sufficient material had come to light to allow the recognition of developmental stages and the elucidation of the complete life cycle (Huys and Boxshall, 1993). Thus, within the span of a decade, Tantulocarida moved from a new class entity with very little known about it to a completely resolved life cycle – all played out on the pages of JCB.

Cephalocarida.—I think the best example of this serial monography occurred for the class Cephalocarida. JCB has handled 13 publications devoted to that group. These papers have effectively covered almost the entire array of organ systems in that class: in chronological order beginning with the supposed compound eyes already noted above (Burnett, 1981); the central nervous system (Elofsson and Hessler, 1990) [which included a rebuttal of the paper of Burnett (1981) concerning remnants of compound eyes]; antennae (Elofsson and Hessler, 1991); the main excretory organs (Hessler and Elofsson, 1991); neurons (Elofsson, 1992); the digestive system (Elofsson et al., 1992); cuticle (Elofsson and Hessler, 1994); podocytes (Hessler and Elofsson, 1995); the reproductive system (Hessler et al., 1995); tegumental glands (Elofsson and Hessler, 1998); a new genus and species *Hampsonella brasiliensis* Hessler and Wakabara, 2000; the circulatory system (Hessler and Elofsson, 2001); and another new species, *Sandersiella kikuchii* Shimomura and Akiyama, 2008. If bound and published as a single book, these papers would constitute a sizeable monograph.

These 13 articles carried on from where the earlier published monographs on the comparative anatomy, functional morphology, and larval development (Sanders, 1963), and skeleto-musculature (Hessler, 1964) of *Hutchinsoniella macracantha* had left off. Hessler and Elofsson (1999) summarized some of this JCB material in the short chapter they prepared for the Microscopic Anatomy of the Invertebrates, but of course the series of publications in JCB continued on after the deadline for that chapter, so while the 1999 chapter was 16 pages in length, the JCB cephalocarid series constitutes some 174 pages.

Mictacea.—Finally, most of the species for the order Mictacea had their debut in JCB. The order was launched with a triple-header: Sanders et al. (1985) described a new genus and species, *Hirsutia bathyalis*, from the deep-sea, tropical Atlantic; Bowman and Iliffe (1985) described another new genus and species, *Mictocaris halope*, from marine caves on Bermuda; and Bowman et al. (1985) pulled the first two papers together and erected a new order, Mictacea, within Peracarida. In recognition of the significance of JCB in the birth of Mictacea, Just and Poore (1988) described in our journal a second species of *Hirsutia*, *H. sandersetalia*; rather startlingly, this species was discovered on the other side of the world from *H. bathyalis*, in the Bass Strait between Tasmania and continental Australia. Such a disjunct distribution promises more discoveries to come, as is indeed beginning to occur, e.g., see Gutu (1998, 2001), Gutu and Iliffe (1998), and Ohtsuka et al. (2002).

Other Noteworthy Publications

Firsts for JCB

An overview of the first occurrences of subject themes within JCB tells us something of the progress and highlights through these last 30 years. These ''first'' match well the advances that have occurred in the field as a whole.

Fossils.—The first paper in JCB that dealt with fossils alone (Bishop, 1983) appeared in volume 3, and although the succeeding papers in that field were at first slow to come in, articles that deal with paleobiology now constitute a steady stream of submissions. Almost every issue contains at least one contribution dealing in whole or in part with fossil material. This reflects the increasing importance of fossil studies in the evolution and phylogeny of the crustaceans.

Cladograms.—Cladistic analysis got a relatively late start in the field of carcinology, long after workers in other groups of arthropods had employed it. Why this was so, I cannot say, but perhaps the overwhelming acceptance of certain paradigms concerning crustacean relationships had something to do with it (see Whittington and Rolfe, 1963). The first ''cladograms'' in the crustacean literature appeared in several papers in Schram (1983), but only two chapters in that volume tied explicit character state expressions to specific clades and thus can be considered truly cladistic (Grygier, 1983, for ascothoracidans; Sieg, 1983, for tanaidaceans). The use of cladistics obtained further promotion with the efforts of Schram (1984, 1986). However, the first paper in JCB to utilize a true cladistic analysis, in this case of the anomuran genus *Aegla*, was that of Martin and Abele (1986). However, such was the state of the art in those days that the Martin and Abele cladogram, generated with PHYSIS (a program no longer used), was backed up with a phenogram derived from a phenetic

UPGMA (the latter is hardly ever seen any more, at least in a phylogenetic context).

Matters Molecular.—The first paper published in JCB in the field of molecular phylogeny (Kim and Abele, 1990) employed a limited taxon sample of decapods and used 18S rRNA. This article was followed by many more molecular-sequence generated phylogenies including some additional firsts: a high impact paper involving cirripedes and 18S rDNA (Spears et al., 1994), which was one of the first papers anywhere to pay some attention to secondary molecule structure; a 12S rDNA generated phylogeny of Branchiopoda (Hanner and Fugate, 1997); and the first molecular phylogeny of isopods, albeit employing a limited taxon sample, but using three genes, 12S-, 16S rDNA, and CO1 (Wetzer, 2002). The first JCB phylogeny derived from electrophoretic data was applied to penaeids (Tam and Chu, 1993), a group that continues to attract controversy concerning their phylogenetic relationships and their generic classification (see Dall, 2007).

The first JCB contribution in what would come to be called genomics (Neigel et al., 1991) came relatively early and involved the genus *Menippe*. This paper outlined techniques for cloning and screening and was an early effort in the field as a whole. More extensive sequencing capabilities have allowed the field to blossom, and now papers in this area are featured in their own section in our Tables of Contents.

Use of Color.—The first use of color in JCB occurred in a description of an atyid shrimp from Taiwan (Hung et al., 1993). This particular paper came from a laboratory that has employed increasing use of color photographs in connection with species descriptions in not only JCB, but other outlets as well. Costs to reproduce color have plunged in recent years with the implementation of digital production, and the use of color is now becoming more pervasive.

Controversies

JCB has seen its share of controversies play out on its pages.

The small contretemps concerning eye remnants in cephalocarids was mentioned above. However, one of the earliest papers to explicitly challenge orthodoxy was Bowman (1984), who reviewed the matter of the polarity of eye evolution and concluded that sessile eyes were the more primitive condition as opposed to what he believed were the more derived stalked eyes.

Along these lines Dahl (1983) had proposed elsewhere an unusual interpretation of how the carapace was formed, advocating a process involving dorsal segmental fusion in the thorax. This prompted a robust rebuttal by Newman and Knight (1984), who argued for the traditional view that the carapace is an outgrowth from the posterior edge of the cephalic shield. However, this issue of carapace origin is a vexatious one as evidenced by the papers of Casanova (1991, 1993), who presented evidence that the carapace is an outgrowth not of the maxillary segment, but rather of the antennal segment.

In an entirely different vein, Chapman and Carlton (1991, 1994) took up the difficult issue that plagues biogeography – how does one determine whether a species might or might not be an invasive one – and laid out some criteria, or predictive attributes, by which such assessments could be made. Chapman and Carlton were explicitly dealing with the isopod *Synidotea laevidorsalis* in the Australia fauna. However, Poore (1996) questioned the effectiveness of the criteria of Chapman and Carlton, arguing against each one of their attributes. Biogeography is a science often wanting for testable hypotheses, and while in the case of *S. laevidorsalis* the issues still remains clouded, nevertheless the effectiveness of the Chapman and Carlton concepts remain to be explored.

Items of Special Interest

Randomly Chosen Highlights.—Thumbing through the past issues of JCB reminds me of sampling a smorgasbord buffet; lots of dishes, each tantalizing in its own way. And just as with that kind of food selection, it is impossible to eat from every single dish; while each person samples different items on offer. So too, I might offer a few published items that appealed to me personally, but I think also represent the wide array of offerings in systematic and evolutionary biology that JCB has published.

For some years, the journal bestowed a Best Paper Award for a particular volume. The second such Best Paper Award (Felgenhauer and Abele, 1983) involved a study of feeding in the caridean shrimp, *Atya innocous*. This article is noteworthy because not only is it a detailed study of the anatomy and functional morphology, it is also a visually beautiful paper. The authors used a distinct blend of light and electron microscopy (and in the latter both TEM and SEM) and tied these together in composite figures with line drawings of the relevant structures. The SEMs are especially breath taking, and a few years later Felgenhauer (1987) documented the technique employed in an often cited, ‘‘how-to’’ paper, which still bears reading by any student seeking to produce the highest quality SEMs. The original 1983 paper had a sequel (Felgenhauer and Abele, 1985), equally as stunning in appearance, focusing on internal morphology of the foregut and placing this anatomy in a phylogenetic context. These papers were indeed research set in a ‘‘big picture’’ that was further expanded upon in Abele and Felgenhauer (1986) and Felgenhauer and Abele (1989).

A fascinating pair of papers in JCB involved Rhizocephala. Ritchie and Høeg (1981) elucidated for the first time the life cycle of the kentrogonid *Lernaeodiscus porcellanae*. This effort was followed by the work of Høeg (1990), which provided information concerning a new type of life cycle in the akentrogonid rhizocephalans. These together proved to be benchmark papers that marked the beginning of a series of contributions published in a variety of sources that helped to resolve not only matters of life cycles, but also the phylogenetic affinities of Rhizocephala. The akentrogonids up until 1990 usually had been viewed as a paraphyletic assemblage, but this life cycle work immediately led to a revision of the group (Høeg and Rybakov, 1992) and then continued through a whole host of papers (cf. Høeg, 1992) to pay dividends, culminating in understanding the evolution of the order not only in terms of comparative anatomy, but also molecular systematics and developmental biology of the thecostracan maxillopodans (Pérez-Losada et al., 2002; Glenner et al., 2010).

Not only as an editor, but also as a scientist I have a strong affinity to papers involving phylogenetic analyses. If they employ cladistics in some kind of added-value sense, extending beyond just assessing phylogenetic relationships, so much the better. One such paper was Kitaura and Wada (2006) that employed the phylogenetics of the ocypodid crab genus *Iloplax* to elucidate the evolution of waving behaviors in the males. The resolved cladogram derived from 12S and 16S rRNA revealed sympatric species patterns that accounted for divergent waving behaviors. This article reminded me of another set of publications some years before (McLaughlin and Lemaitre, 1997; McLaughlin et al., 2004) in which the authors employed cladograms to elucidate possible patterns of carcinization in Anomura and pose alternative hypotheses derived from adult and larval comparative anatomy. Olesen (2007) used much the same strategy in his review of phylogenetic patterns in the evolution of phyllopodous limbs in Branchiopoda, in this case with an elegant set of SEMs of limbs, larvae, and embryos. In each of these instances, cladistics was not the end of the paper, rather merely a means towards elucidating the evolution of morphology and behavior.

Traditional uses of cladistic analysis abound in the pages of JCB, wherein phylogenetic analysis has lead to not only patterns of relationships within groups, but also major taxonomic revisions. To try and list them all would risk inadvertently leaving some out and cause offense. Nevertheless, these sorts of papers, e.g., Poore (2001), Myers and Lowry (2003), are real "bread-and-butter" publications for JCB and will continue to appear in our pages.

Two Overlooked Gems.—Finally, in any collection survey, there will always be papers that stand out for a reviewer not because they represent necessarily some quantum element in advancing knowledge, but because they have a certain *je ne sais quoi*. So it is with me.

One such paper is Mark Grygier's translation of Starobogatov (1988). The original paper was in Russian. The classification scheme for crustaceans proposed in this contribution is idiosyncratic to say the least. Yet the paper fascinates because, for me, it offers an insight into another mindset, that from a different culture and distinct way of looking at things quite at odds with what one encounters in the "western" viewpoint. Starobogatov studied arthropod anatomy with a singular perspective: on one hand influenced undoubtedly by the great, Russian comparative anatomist, V. N. Beklemishev, who had a distinctive and insightful overview of invertebrate anatomy well-exemplified by the first volume on "promorphology" in his monumental text, "Principles of Comparative Anatomy of Invertebrates;" and on the other hand by the somewhat Aristotelian, dialectic reasoning of Soviet science. It is not a matter of being correct or wrong – it is simply an alternative viewpoint from the reductionist, cause-and-effect approach more familiar to us schooled in the Western tradition.

This JCB paper has been virtually ignored. Yet, when I look at it today, I see things that are reflected in some of the current molecular trees recently published (Koenemann et al., 2010; Regier et al., 2010). For example, Starobogatov's Infraclass Spelionectioni versus today's Xenocarida, uniting Remipedia and Cephalocarida; and Starobogatov's classes Ascothoracioides and Halicynioides versus the separation of thecostracans from copepods in distinctly separated clades (effectively obliterating Maxillopoda as a valid group). Even in idiosyncrasy there can be flashes of insight. This translation of Starobogatov's paper illustrates nicely that when we focus on orthodoxy with too rigid a mindset, we risk overlooking some alternative hypotheses that may have merit.

A purely comparative anatomical paper by Conlan (1995) represents another such overlooked gem for me; it has apparently generated little response. In this article, Conlan studied the evolution of claws on the second gnathopods of the corophioid amphipod genus *Microjassa*. The diversity in claw form in these species is quite amazing, and in her paper the cladistic analysis neatly encapsulated the evolution of form and related it to biogeographic distribution in a context of climate shifts in the Tertiary. The impact factor of this paper (Sainte-Marie, 2010) is rather low, and I don't understand why – it is an elegant study, and one that should serve as a model for similar efforts in other groups. For example, such claw variation reminded me of what one can see on the terminal elements on the maxillules of remipedes.

What Does the Future Hold?

Predicting what the future holds is fraught with uncertainty. Hence, reading too much into any predictions concerning the future of carcinology has to be taken with a strong dose of caution. For example, when I look at papers such as Koenemann et al. (2010) and Regier et al. (2010), I see things that one could not have predicted 30 years ago.

For several years, JCB used to give best paper awards for a volume; that was discontinued several years ago. Today we have other ways of measuring importance and interest in published articles. With bibliometric algorithms, we can now more directly determine just what attracts reader interest, e.g., see JCB 30(1): 158, "Top 10 most-accessed articles in JCB during 2009." From such a list we might suspect that for JCB genomics will figure more prominently in carcinology; two of the top 10 on that list (Buhay, 2009; Buhay and Crandall, 2009) deal in whole or in part with gene product analysis. One might also expect that research on crayfish will hold interest into the future; six of the 10 most accessed articles from last year deal with various aspects of the biology of Astacidea. And yes, we will also continue to publish alpha-taxonomy: two of the top 10 papers deal in some way with new species descriptions.

As an editor, I would like to see more publications in JCB dealing with development – especially in connection with studies of non-model organisms, early embryology, *Hox*-gene expression, and comparative developmental biology. I realize, however, that other journals in the field of evo-devo might provide alternative venues for young authors. I would also like to see more total evidence approaches to understanding the phylogeny of the crustaceans as a whole, as well as of individual groups of crustaceans. I still look forward to the day when JCB includes papers dealing with pycnogonids and merostomes – in the spirit of advancing knowledge of aquatic arthropods *sensu lato*.

Editors, like readers, have to be open to the possibility of something entirely new and different: new classes and/or orders? – new techniques of analysis? – new insights into old problems? As long as people support The Crustacean Society with their memberships, JCB will continue with its mission: to advance the study and dissemination of knowledge about crustaceans.

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