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AN APPRECIATION OF THE CONTRIBUTION OF ARTHUR HUMES TO COPEPOD SYSTEMATICS

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Arthur Humes had a long and distinguished career in biology. His first publication was in 1938 and his first paper on copepods was in 1941. Since then he has produced an incredible 252 publications on copepods. Arthur is best known to the members of The Crustacean Society as the founding editor of the *Journal of Crustacean Biology* but, in the copepod research community, he is recognised as being responsible for opening up one of the four main fields of copepod systematics: the taxonomy and biodiversity of copepods associated with, and parasitic on, marine invertebrates. Starting virtually from scratch, building a new field has required an immense volume of descriptive taxonomy. By providing this he has established the basic framework of knowledge on these groups—the knowledge base, which has, in recent years, provided phylogeneticists with an incredibly rich source of data.

Arthur Humes's success in opening up the field of invertebrate associates depended initially on his recognition that virtually any marine macroinvertebrate was a potential host to copepods. In 1993, in the Maxilliped lecture given when he was president of the World Association of Copepodologists, Humes calculated that associated copepods are known from only 1.14% of the 151,400 species of potential marine invertebrate hosts worldwide (Humes, 1994). On these calculations, the amount of descriptive taxonomy remaining to be done is enormous.

His Methods

During his career, Humes himself surveyed a huge range of invertebrate host taxa and developed an extraction technique, which was to prove suitable for coaxing the copepods out from many hosts. This method, as applied to the extraction of xarifiid copepods from hard corals (Humes and Dojiri, 1982) is repeated here: *immediately on collection in the field each colony or fragment of coral is isolated in a plastic bag. In the laboratory the coral and sea water are placed in a bucket to which sufficient 95% ethanol is added to make an approximately 5% solution. The coral is left in this solution at ambient temperature for several hours or over night. Then the coral is thoroughly rinsed by shaking well and the wash water is poured through a fine net (120 holes per 2.5 cm, each hole approximately 100 μm square). The copepods are then picked from the sediment retained in the net.* It appears that the dilute alcohol, together with the accumulating products of decomposition, stimulates the copepods to leave the polyps of the coral host, and they fall to the bottom of the container. In comparison, rapid washing of the freshly collected corals usually yielded very few xarifiids (Humes and Dojiri, 1982). This method can be applied equally to many other host groups, such as soft corals, echinoderms, sponges etc.

In addition to his extraction method, Humes also pioneered various improvements in methods for the microscopic study of copepods. A much-cited methods paper is Humes and Gooding (1964) in which the hanging-drop slide method is described in detail. In this short paper Humes and his brilliant student, Richard Gooding, recommended the use of lactic acid as the best clearing agent for the preparation of temporary mounts for whole or dissected copepods. They also recommended that dissections be carried out in a drop of lactic acid on a 22-mm coverslip cemented to a wooden slide with a bored central hole 15 mm in diameter. The preparation is then ready for examination under the compound microscope by inverting the slide. One of the major advances of this method is that a single specimen can usually provide a full set of observations of all appendages. Humes and Gooding explicitly stated another major advantage of this technique is that it causes

Table 1. New copepod taxa authored or co-authored by Arthur Humes (*: includes one subspecies).

Decade	Number of new species	Number of new genera	Number of new families
1941–1950	4	1	–
1951–1960	43	6	3
1961–1970	172*	23	–
1971–1980	166	59	4
1981–1990	197	29	4
1991–2000	119	33	7
Totals	701*	151	18

little or no compression of the copepods or their dissected parts—a problem that plagued the taxonomic studies of many copepod researchers before 1964 (and still does). They also noted that staining is usually undesirable in this kind of mount and that phase-contrast microscopy may be used. In all these respects Humes and Gooding pioneered the best modern practice, except that the development of differential interference contrast microscopy has essentially replaced phase contrast microscopy.

His Output

Arthur Humes was a sterling systematist and showed a truly astounding level of career productivity. In the course of nearly 60 years research on copepods, Arthur has established 18 new families, 151 new genera, 700 new species, and 1 new subspecies (Table 1). This amazing contribution to copepod taxonomy is one of the greatest taxonomic efforts ever accomplished by a single individual in the field of Crustacea. In years of highest productivity his output of new species descriptions would amount to one per week (Fig. 1) as for example in 1973 when he published the first revision of the Lichomolgoidea with Jan Stock (Humes and Stock, 1973), or in 1982 when he produced (alone or jointly) major contributions to the systematics of the Taeniacanthidae, Xarifiidae, and Rhynchomolgidae (Dojiri and Humes, 1982; Humes, 1982a, b; Humes and Dojiri, 1982). Arthur's taxo-

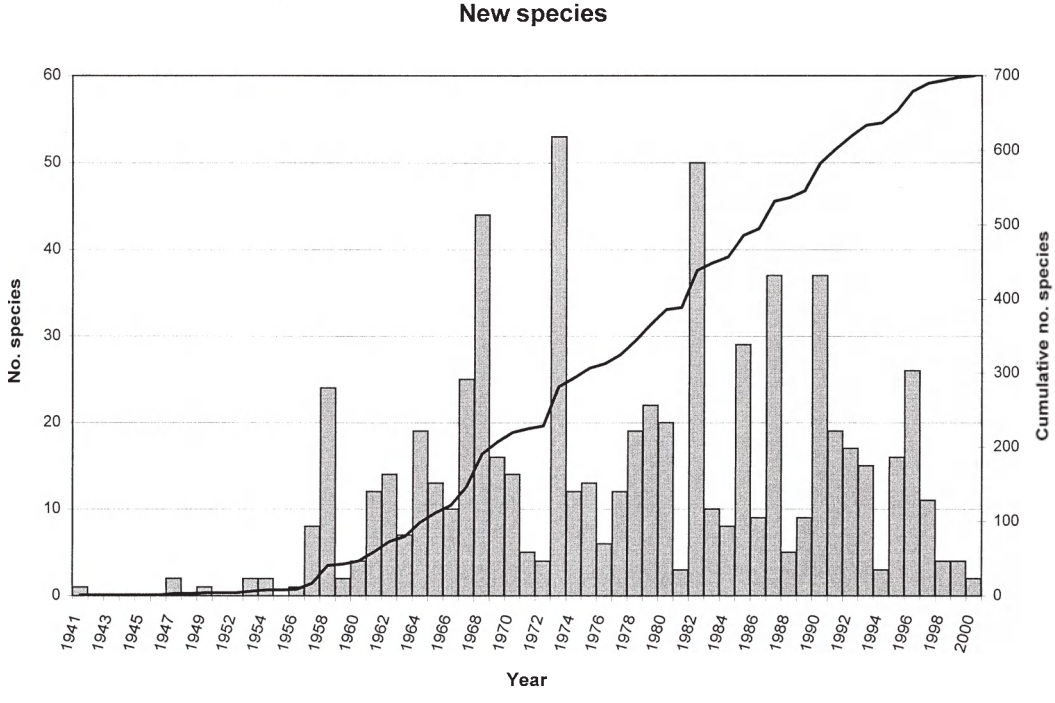

Fig. 1. Number per year and cumulative number of new species described by Arthur Humes between 1941 and 2000.

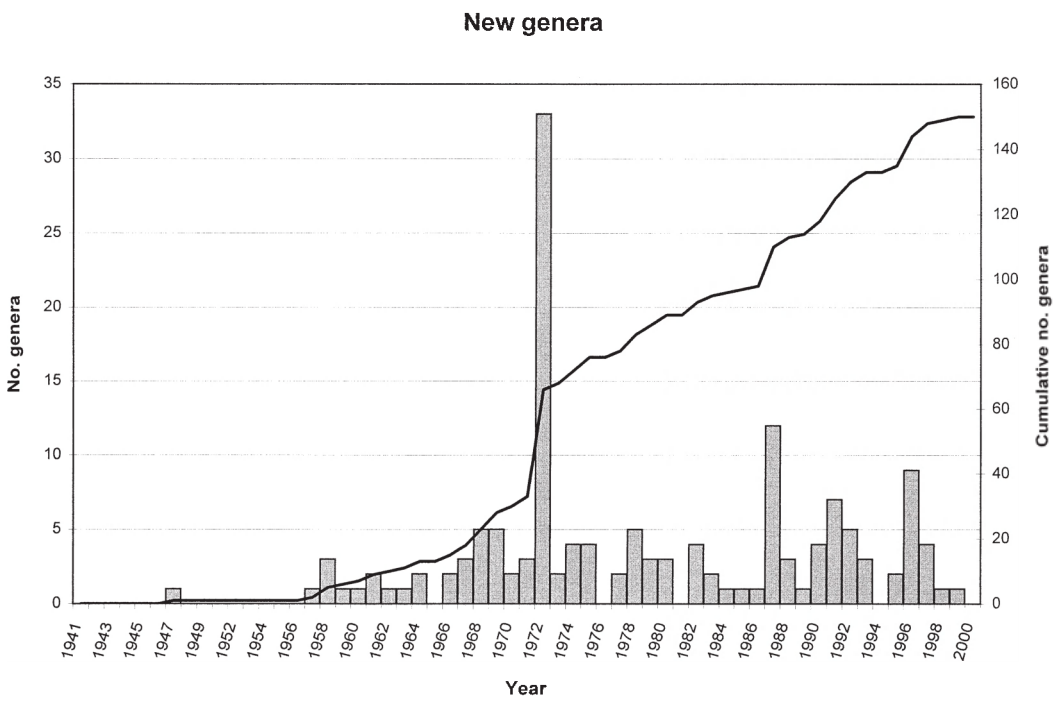

Fig. 2. Number per year and cumulative number of new genera described by Arthur Humes between 1941 and 2000.

nomic work was built on a solid base of massive collections which enabled him to study the variability within species and between geographical areas and hosts. It is therefore not surprising that nearly all of his species have successfully stood the test of time. In fact, only one genus (*Metaxymolgus* Humes and Stock, 1972) and two species (*Sciaenophilus inopinus* Humes, 1957; *Oncaea praeclara* Humes, 1988) have been synonymized since, the last two being representatives of groups Arthur was less acquainted with, the fish parasites and the marine plankton.

As the preeminent authority in the field Arthur Humes received numerous collections, foremost amongst these were the copepods collected from hydrothermal vents and cold seeps. More importantly, Arthur himself accumulated with unrelenting stamina a stupendous amount of material during his fieldwork in West Africa, Madagascar, the Moluccas, Enewetak Atoll, the Great Barrier Reef, and New Caledonia. Although the actual figure is undoubtedly higher, specimen counts based on his published papers from 1955 onwards suggest that Arthur Humes (and his collaborators) sorted and examined over 300,000 individual copepods! On average, this accounts to 130 copepods per week over a 45-year period (Fig. 3).

Arthur remained extraordinarily energetic, even at a later age, and this is best demonstrated by the remarkable fact that nearly half of his new species and genera were described during his 20-year tenure as Editor of the *Journal of Crustacean Biology* between 1980 and 1999 (Figs. 1, 2).

The Diversity of His Research

Sixteen phyla of invertebrates are utilized as hosts for copepods (Huys and Boxshall, 1991). Arthur Humes almost covered this entire spectrum and published on twelve of them (Fig. 4), including the first records of copepods occurring on the lophophorate phyla Phoronida and Brachiopoda (Boxshall and Humes, 1988; Humes and Boxshall, 1988) and new species from bizarre host groups such as the flatworms (Humes, 1997) and the vestimentiferans (Humes, 1973a; Humes and Dojiri, 1980, 1981). Of all groups his descriptive work on the poecilostomatoids and siphonostomatoids associated with cnidarian hosts will remain as an enduring

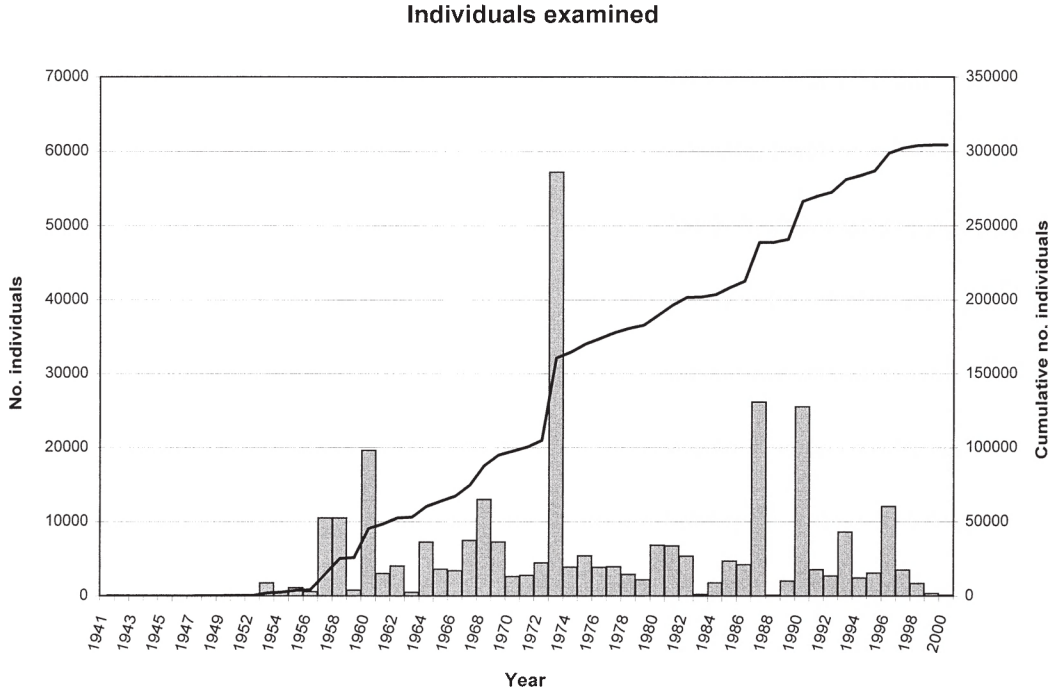

Fig. 3. Number per year and cumulative number of individuals examined by Arthur Humes between 1941 and 2000.

monument. In 1986, Humes estimated the number of described copepod species associated with cnidarians at 416, but to his credit, he forgot to mention that 282 (or 68%) had been described by himself (Humes, 1985b). In the remaining years of his career Arthur added another 110 species, bringing his personal total for this host group to 392 species. The evolutionary success of the copepod-cnidarian association did not distract his attention from copepods occurring on other invertebrate groups such as the echinoderms (137 species), molluscs (54 species), and to a lesser extent the crustaceans (20 species) and the polychaetes (14 species) (Fig. 4).

Although the great majority of Arthur's material was collected by snorkeling and SCUBA diving in shallow subtidal habitats, his fascination for the group led him to cover the entire depth range of associated copepods. His early research in the 1940s and 1950s focused primarily on crustacean and molluscan hosts from easily accessible habitats. Surveys of marsh crabs, mud shrimps and even the edible mussel in North America and West Africa resulted in the unexpected discovery of several harpacticoids and provided Arthur with the impetus to extend his search for copepods to both the sublittoral environment and to other host groups such as the cnidarians and echinoderms. With the exception of the occasional paper on deep-sea copepods (Humes, 1973a, 1974; Humes and Grassle, 1979), his career went full circle in the 1980s and 1990s when he received the copepods collected at hydrothermal vents in the eastern Pacific and the mid-Atlantic and deeply immersed himself in a totally unknown fauna. Over the years, the examination of nearly 60,000 specimens from these habitats culminated in the description of three new families, 18 new genera, and 61 new species (Humes and Segonzac, 1998; Humes, 1999a).

Copepods occur on vertebrate as well as invertebrate hosts, but Arthur rarely published on associates of vertebrates. In over five decades he published only five taxonomic papers on vertebrate associates (Humes, 1957, 1964, 1965; Humes and Rosenfield, 1960; Gooding and Humes, 1963), the most unusual of these being the description of a new harpacticoid species, *Harpacticus pulex* Humes, 1964, found on the sloughed skin of a porpoise and a manatee in Florida.

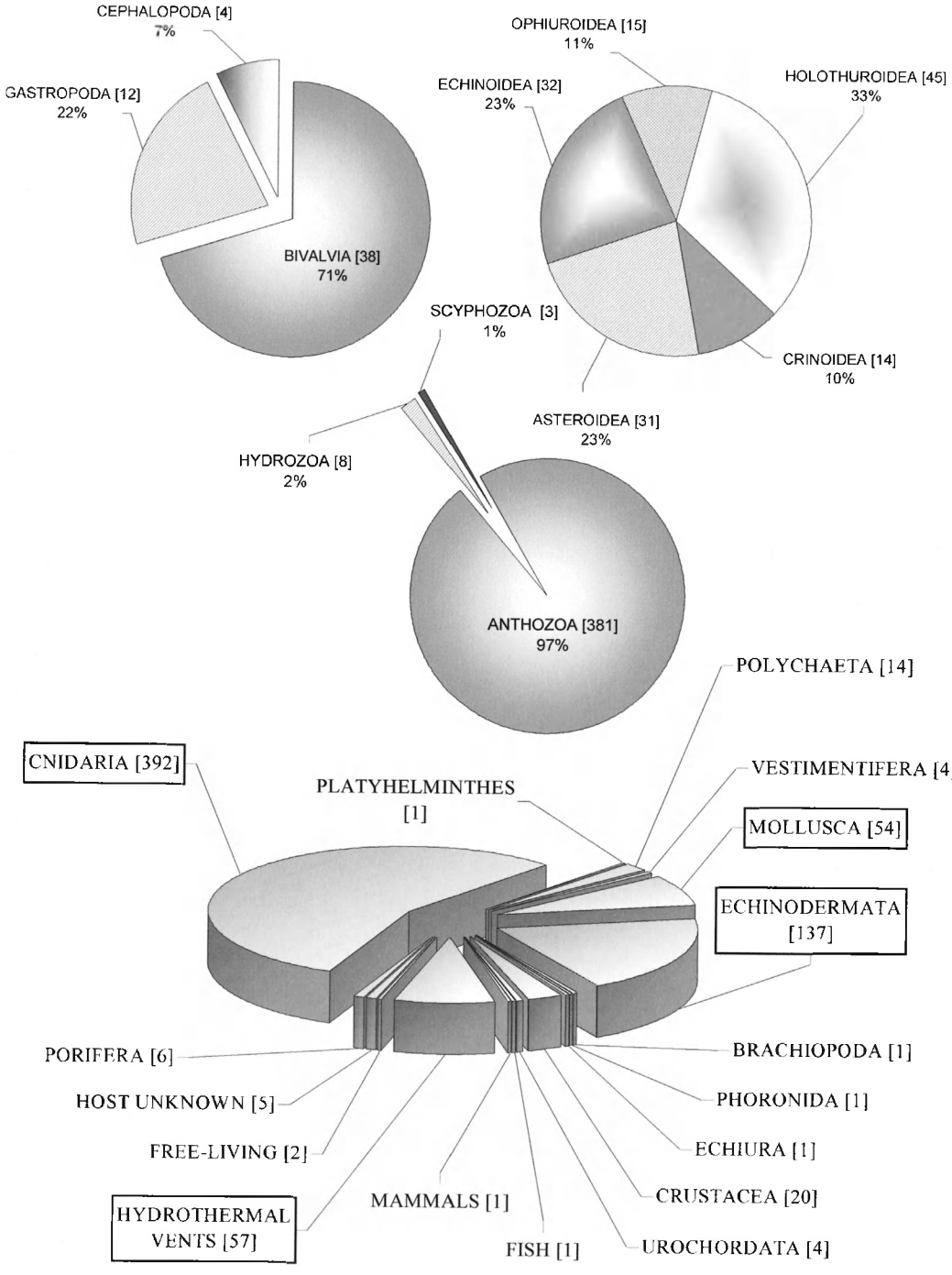

Fig. 4. Pie chart (below) displaying contribution of each host category/habitat in Arthur Humes's research. Relative importance of individual classes in most important host phyla (Cnidaria, Echinodermata, Mollusca) displayed in separate pie charts (upper). All pie charts based on number of new copepod species described (indicated in square brackets).

Table 2. List of copepod orders and families containing new species established by Arthur Humes. Family names in parentheses indicate the two species established by Humes that were subsequently synonymised. The inclusion of the Ascidicolidae is based on recognition of the affinities of the previously unplaced genus *Gomphopodarion* Humes, 1974. [*: Includes one subspecies.]

CALANOIDA		POECILOSTOMATOIDA		SIPHONOSTOMATOIDA	
Diaptomidae	2	Anchimolgidae	84	Asterocheridae	41
Ridgewayiidae	1	Anthessiidae	15	Brychiopontiidae	1
		Catiniidae	1	(Caligidae)	(1)
CYCLOPOIDA		Clausidiidae	22	Cancerillidae	3
Ascidicolidae	1	Erebonasteridae	4	Coralliomyzontidae	6
Cyclopidae	3	Lamippidae	1	Dirivultidae	52
Cyclopinidae	2	Lichomolgidae	41	Ecbathyriontidae	1
Lernaeidae	1	Lubbockiidae	1	Megapontiidae	1
Notodelphyidae	4	Macrochironidae	9	Micropontiidae	1
		Myicolidae	7	Nanaspididae	11
HARPACTICOIDA		Mytilicolidae	2	Nicothoidae	1
Ameiridae	1	Octopicolidae	4*	Stellicomitidae	9
Cancrincolidae	4	(Oncaeidae)	(1)		
Canuellidae	2	Pseudanthessiidae	24	UNPLACED GENERA	
Canthocamptidae	2	Rhynchomolgidae	187	*Parangium* Humes, 1985	1
Diosaccidae	1	Sabelliphilidae	9	*Bythocheres* Humes, 1988	1
Harpacticidae	1	Serpulidicolidae	1		
Peltidiidae	1	Synapticolidae	28		
Porcellidiidae	1	Synaptiphilidae	1		
Tegastidae	5	Taeniacanthidae	12		
Tisbidae	4	Thamnomolgidae	4		
		Vahiniidae	2		
MISOPHRIOIDA		Xarifiidae	76		
Misophriidae	1				

Altogether Humes published on six of the ten currently recognised orders of copepods (Tables 2, 3) including describing a new marine calanoid, *Ridgewayia fosshageni* Humes and Smith, 1974. This species was observed forming free-swimming aggregations in the immediate vicinity of the sea anemone *Bartholomea annulata* Lesueur, although they were never observed resting on or feeding on the anemone (Humes and Smith, 1974). These aggregations might now be categorised as swarming behaviour, and the possibility of association with the anemone requires further experimental verification. His recent work on hydrothermal vent copepods also led Arthur into describing new free-living members of the marine families Cyclopinidae (order Cyclopoida) and Misophriidae (order Misophrioida), a project that was completed just before his death (Humes, 1999b).

While the majority of Arthur's contributions to copepods were purely taxonomic, the collection and processing of vast numbers of copepods also enabled him to study their development in a variety of families such as the Temoridae in the Calanoida, the Clausidiidae in the Poecilostomatoida, and the Tisbidae in the Harpacticoida (Humes, 1955, 1960, 1986c). Similarly, his survey of numerous hosts led him to demonstrate another phenomenon, that of the multiple associations. Humes showed that one host individual or colony may frequently support more than one copepod. A striking example, but not unique in its kind (Humes, 1994), is the hard coral *Acropora hyacinthus* (Dana), which harbours nine poecilostomatoid species. Arthur's research revealed that each of the 12 cnidarian hosts in New Caledonia and 13 hosts in the Moluccas had at least five species of associated copepods. This observation illustrates that, particularly in tropical and subtropical areas, copepod diversity is likely to exceed invertebrate host diversity, often by a factor five or higher.

HARPACTICOIDS, OR HOW IT ALL STARTED

Arthur's interest in associated copepods was stimulated by the discovery of a new harpacticoid in the gill chamber of marsh crabs when he was studying their nemertean parasites as part of his Ph.D. at Lousiana State University (Humes, 1941). This very first new copepod, *Cancrincola plumipes*, was a rep-

Table 3. List of copepod orders and families containing new genera established by Arthur Humes. The inclusion of the Ascidicolidae is based on recognition of the affinities of the previously unplaced genus *Gomphopodarion* Humes, 1974.

CYCLOPOIDA		POECILOSTOMATOIDA		SIPHONOSTOMATOIDA	
Ascidicolidae	1	Anchimolgidae	27	Asterocheridae	12
Cyclopinidae	1	Catiniidae	1	Brychiopontiidae	1
Notodelphyidae	1	Clausidiidae	1	Cancerillidae	2
		Erebonasteridae	2	Coralliomyzontidae	4
HARPACTICOIDA		Lichomolgidae	6	Dirivultidae	13
Cancrincolidae	1	Lubbockiidae	1	Ecbathyriontidae	1
Canthocamptidae	1	Macrochironidae	1	Nanaspididae	1
		Myicolidae	1	Nicothoidae	1
		Octopicolidae	1	Stellicomitidae	5
		Pseudanthessiidae	3		
		Rhynchomolgidae	38	UNPLACED GENERA	
		Sabelliphilidae	6	*Parangium* Humes, 1985	
		Synapticolidae	5	*Bythocheres* Humes, 1988	
		Taeniacanthidae	3		
		Thamnomolgidae	3		
		Vahiniidae	1		
		Xarifiidae	4		

resentative of the Ameiridae (currently classified as the family Cancrincolidae), and Arthur returned to publish on this group on several subsequent occasions when surveying terrestrial crabs along both sides of the central Atlantic. The genera *Cancrincola* Wilson, 1913, and *Antillesia* Humes, 1958, utilize primarily Gecarcinidae (true land crabs) as hosts and are restricted to the Atlantic basin. Stimulated by his initial discovery, Arthur extended his search for harpacticoids to another group of terrestrial crabs, the Grapsidae, and discovered that at least in the Indo-Pacific a different genus, *Pholetiscus* Humes, 1947, was associated with this host group (Humes, 1956). Arthur's recognition of the canthocamptid affinities of this new genus was significant because it demonstrated that the primarily free-living Harpacticoida had entered into association with land crabs at least twice during their evolutionary history.

During his career Arthur Humes described 23 species of harpacticoids belonging to ten different families (Table 2) and utilizing eight different host groups: Crustacea, Hydrozoa, Scyphozoa, Scleractinia, Alcyonacea, Bivalvia, Holothuroidea and Echinoidea. Harpacticoids have generally been considered to be only rarely associated with invertebrates, but Humes's studies have firmly established that at least in the modified families Tegastidae, Peltidiidae, and Porcellidiidae several lineages have entered into symbiotic relationships with cnidarians, echinoderms, and hermit crabs. The latter group offers a good example of independent colonization by three different families of harpacticoids, the Tisbidae, Porcellidiidae, and Canuellidae (Humes and Ho, 1968a, b).

COPEPODS AND CNIDARIA– HIS LIFETIME OBSESSION

Although Arthur published on a plethora of host groups, it was the Cnidaria that was to occupy him for most of his scientific career. Copepods are associated with all three classes of Cnidaria, the Hydrozoa, the Scyphozoa, and the Anthozoa, and Humes published on all three of them (Fig. 4). Humes's studies of the poecilostomatoid family Macrochironidae contributed significantly to the systematics of copepods associated with the polyp stages of hydroids (e.g., Humes, 1966, 1977; Humes and De Maria, 1969) and the scyphozoan medusae (e.g., Humes, 1969, 1970), but it is his work on the Anthozoa that deserves special mention. His first paper on this group was not until 1958 when he described a new species of *Lamippe* Bruzelius, 1858, from West African pennatulaceans, but what followed after his fieldwork in Nosy Bé was a real deluge of new taxa, representing 251 new species associated with hexacorallian hosts and 130 new species with octocorallian hosts. Except for the Ceriantharia and the Corallimorpharia, Arthur Humes surveyed hosts of all major anthozoan groups (Fig. 5). No copepodologist before him has dominated

Table 4. Number of specimens examined by Arthur Humes for each host category.

Porifera	357
Cnidaria	103,127
Anthozoa	96,367
Alcyonacea	34,344
Gorgonacea	17,031
Pennatulacea	384
Stolonifera	844
Telestacea	1,896
Actiniaria	3,900
Antipatharia	2,966
Scleractinia	33,734
Zoanthidea	1,268
Hydrozoa	5,592
Scyphozoa	1,168
Platyhelminthes	9
Polychaeta	2,590
Vestimentifera	236
Mollusca	33,069
Bivalvia	30,080
Cephalopoda	382
Gastropoda	2,607
Echinodermata	86,408
Asteroidea	18,196
Crinoidea	7,684
Echinoidea	10,703
Holothuroidea	19,244
Ophiuroidea	30,581
Brachiopoda	11
Phoronida	3
Echiura	5
Crustacea	18,572
Urochordata	860
Fish	49
Mammals	158
Hydrothermal vents	57,922
Free-living	1,628
Host unknown	859
Total	305,863

this field as Arthur did, and we suspect none ever will again.

Among the various groups of the Hexacorallia, the Scleractinia, or hard corals, have more copepod associates than any other group. The vast majority of these associates belong to the Anchimolgidae, Rhynchomolgidae, and Xarifiidae. Members of the Anchimolgidae are exclusively associated with scleractinian corals and are currently accommodated in 28 genera—27 of which having been described by Humes and the remaining one being named after him by Sebastian and Pillai (1973) [*Humesiella*]. Arthur named no less than 84 species of Anchimolgidae which represents nearly 95% of the total number described.

The Xarifiidae is a good example of the progress stimulated by Humes's research. Xarifiids are internal parasites of both hermatypic and ahermatypic scleractinian corals and had never been reported before 1960. They inhabit the gastrovascular cavities of the coral polyps and can best be extracted using the techniques described above (Humes and Dojiri, 1982). This family had humble beginnings: in 1960 Humes described just two species, which he placed in a new genus, *Xarifia*, the type genus of his new family. Currently the Xarifiidae comprises 84 species in four genera, and Humes is author or co-author (with either Ju-shey Ho or Masahiro Dojiri) of all four genera and the great majority (76) of the 84 species (Humes, 1960b, 1962, 1985a; Humes and Ho, 1967, 1968; Humes and Dojiri, 1982, 1983). The family is incompletely known, for Humes (1985a) mentioned an additional 16 new species in his possession that were represented by too few specimens to allow their description. The distribution of xarifiids is limited by the ecological requirements of their coral hosts, but they occur from the Red Sea-Madagascar area eastward to an arc formed by Japan-Enewetak Atoll-New Caledonia (Humes, 1985a). They are absent from the Caribbean and from the Pacific east of 166°W (e.g., from Hawaii, Moorea and Panama).

The Xarifiidae is a classic example of a family of associated copepods that, once their habitat was discovered and a method to extract them was developed, proved to be both widespread and common. In stark contrast is the family Vahiniidae, also associated with cnidarian hosts, in this case antipatharians, and also established by Humes (Humes, 1967). The family was based on a monotypic new genus *Vahinia* Humes, 1967 and a second species was added to the genus in 1979 (Humes, 1979) but, despite extensive sam-

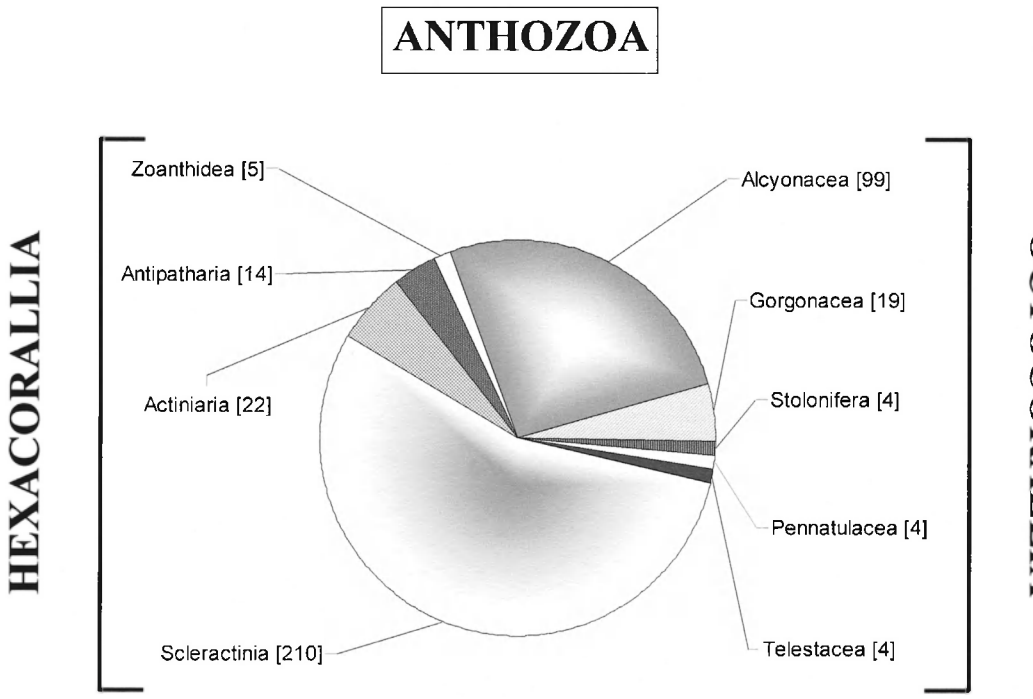

Fig. 5. Pie chart displaying detailed host utilization of new species described by Arthur Humes from hexacorallian and octocorallian anthozoans. Number of new species indicated in square brackets.

pling of antipatharians, more vahiniids have not been collected. The expenditure of sufficient search effort by Arthur Humes now allows us to conclude that these animals are genuinely rare.

Within the Octocorallia, the Alcyonacea, or soft corals, have the greatest number of copepod associates, and as with the scleractinians, our knowledge on this group bears the strong stamp of Arthur Humes's approach to systematics. The first unequivocal association of a copepod with an alcyonacean was reported by Stock and Kleeton (1963) who discovered *Critomolgus bulbipes* (Stock and Kleeton, 1963) on two soft corals in the vicinity of Banyuls. At that time nothing was known about such associations in the tropical Indo-Pacific. However, Humes's extensive fieldwork in Madagascar, New Caledonia, the Moluccas and Enewetak Atoll triggered a series of papers on soft coral associates, and these served to demonstrate that copepods are particularly abundant on alcyonaceans and gorgonaceans. Three decades after the initial discovery of a copepod on a soft coral, 98 copepod species are now known to occur on Indo-Pacific alcyonaceans, 96 of which were described by Humes, solely or jointly with M. Dojiri, B. W. Frost, J.-s. Ho or J. H. Stock (Humes, 1990a, 1996).

The Lichomolgoid Complex

Over his long career Humes exhibited a particular affinity for one family-group above all others, the Lichomolgidae. The enormous numbers of new species and genera added to this family-group by Humes and his collaborators over the years stimulated two major revisionary works. The first revision was published in 1973 in collaboration with Jan Stock (Humes and Stock, 1973), although the new genera and families were validly published a year earlier (Humes and Stock, 1972). In this work three new families, Pseudanthessiidae, Rhynchomolgidae, and Urocopiidae, were established and placed in a new superfamily, the Lichomolgoidea, together with the two existing families, the Lichomolgidae and Sabelliphilidae. These families were distinguished largely on the basis of differences in the segmentation and setation of the first to fifth swimming legs. However, by the mid-1990s

more than 40 new genera had been added to the lichomolgoid complex, and the boundaries between the five constituent families had become blurred. Humes and Boxshall (1996) undertook a further revision of the lichomolgoid complex, excluding the Urocopiidae, and recognized six new families, the Anchimolgidae, Kelleriidae, Octopicolidae, Macrochironidae, Synapticolidae, and Thamnomolgidae. Together with his numerous co-authors, Humes's cumulative contribution to the expansion of knowledge of the lichomolgoid complex is a total of eight new families (excluding the Urocopiidae), 90 new genera, and an amazing 385 new species. These absolute numbers represent 80% of the known families, 67% of the genera, and 68% of the species, respectively.

The Mollusc Parasites

During the 1950s Arthur almost exclusively wrote on copepods associated with molluscs and echinoderms. It was during this period that his first disciple, Roger Cressey, entered his laboratory and jointly worked up the material collected from West African bivalves (Humes and Cressey, 1958a). Meanwhile, Arthur concentrated also on the mollusc associates from Madagascar which resulted in a major contribution the following year (Humes, 1959). Over his career Humes returned many times to the study of parasites of marine molluscs, paying particular attention to the heterogeneous family, the Myicolidae, established without diagnosis by Yamaguti (1936). In 1986 Humes restricted the concept of the family by excluding five genera which he placed in a newly designated family, the Anthessiidae. Humes (1986a) retained only the genera *Myicola*, *Pseudomyicola*, and *Ostrincola* in the Myicolidae and provided detailed diagnoses of both families. Later Humes and Boxshall (1988) added *Parostrincola*, unique within the family in its utilization of an intertidal brachiopod, *Lingula anatina* Lamarck, as host, and Ho and Kim (1992) established two further new genera, one of which, *Exostrincola*, was based on *Ostrincola simplex* Humes, 1958. The myicolids are typically parasites of marine bivalve molluscs, occurring on the gills, in the mantle cavity, and in the intestine of their hosts. Describing these taxa and creating a more robust classification system represents a real contribution to societal needs. Some myicolids are serious pests of commercially cultured bivalves and have been responsible for mass mortality in cultured bivalves (Ho and Yoosukh, 1994; Ho and Zheng, 1994). As the economic importance of aquaculture increases world wide, the basic descriptive taxonomy of these potential pests generated by Humes will provide the platform on which subsequent life cycle and biological research can be built.

Echinoderm Associates–A Lasting Affiliation

All five classes of echinoderms serve as hosts for copepods, and Arthur made major contributions across all five, totalling 137 new species (Fig. 4). He published his first paper on the group in 1958 and continued working on echinoderm associates throughout his career until his death. In fact, his last paper that went to press dealt with the biology and taxonomy of species of *Ophiopsyllus* Stock, Humes, and Gooding, 1963, and *Pseudanthessius* Claus, 1889, associated with ophiuroids in Belize (with Gordon Hendler).

Arthur's research on echinoderm associates serves to demonstrate the sheer abundance of copepods associated with marine invertebrate hosts. Despite his own attempt to estimate the number of copepods (Humes, 1994), their absolute abundance appears to be beyond imagination and certainly beyond calculation. One classic example of the tremendous carrying capacity of these hosts is demonstrated in his first paper dealing with the large tropical basket star *Astroboa nuda* (Lyman) (Humes, 1973b). From three basket stars (approximately 20 cm in diameter) examined, Arthur recovered a staggering 27,209 individuals of *Collocherides astroboae* Stock, 1971, and *Doridicola micropus* (Humes, 1973). Another example is the siphonostomatoid family Stellicomitidae, the first new family recognised by Humes (Humes and Cressey, 1958b). These tiny associated copepods inhabit starfishes and can reach enormous population densities on their hosts. Humes (1971), for example, reported 1,420 individuals of *Stellicomes supplicans* Humes, 1971, on just two individual starfishes only 10 cm in diameter.

In addition to describing four new families associated with echinoderms (Humes and Cressey, 1958b, 1959; Humes, 1974; Humes and Boxshall, 1996), Arthur also contributed

significantly to our knowledge of the Taeniacanthidae. This is a very unusual family in that it utilizes both invertebrates and vertebrates as hosts. The 91 species and 14 genera of taeniacanthids recognized as valid by Dojiri and Cressey (1987) fall into two ecological groups according to host preference. Three genera, *Echinosocius* Humes and Cressey, 1961, *Echinirus* Humes and Cressey, 1961, and *Clavisodalis* Humes, 1970, are associates of sea urchins (Echinoidea). These three genera comprise a total of 14 species which occur only in the Indo-west Pacific and Red Sea and inhabit the oesophagus of their echinoderm hosts. Arthur was author or co-author of 12 of these 14 known species. The remaining 11 genera are widely distributed parasites of marine fishes, both elasmobranchs and teleosts. This family has been extensively studied and was the subject of two revisions. Dojiri and Humes (1982) reviewed the taeniacanthids parasitic on sea urchins in the southwestern Pacific and provided a key to the known species of urchin parasites worldwide. Dojiri and Cressey (1987) revised the entire family and provided a comprehensive diagnosis of the family, a key to genera, and keys to the species parasitic on fishes.

Hydrothermal Vents, Cold Seeps, and the Dirivultid Explosion

The discovery of a specialized fauna associated with the larger invertebrates living at hydrothermal vents and cold seeps provided Arthur Humes with a new challenge in the early 1980s. The family Dirivultidae was established in 1981 (Humes and Dojiri, 1981) based on a single species of a new genus, *Dirivultus* Humes and Dojiri, 1981, collected from a vestimentiferan worm off the California coast. Because of different in-press times, in the preceding year (1980) these authors added a second monotypic genus, *Ceuthoecetes* Humes and Dojiri, 1980, also associated with a vestimentiferan host. During two decades Arthur served as the main recipient for new copepod collections from hydrothermal vents and cold seeps worldwide which enabled him to publish extensively on the subject, including no less than 15 papers dealing with the Dirivultidae. Due to his single-handed efforts this family has now grown to comprise twelve genera and 53 species, if we include *Fissuricola* Humes, 1987, which was not originally placed in this family by Humes (1987). The dirivultids are the dominant group of copepods at most hydrothermal sites in the eastern Pacific, in the Marianas Back-Arc Basin, and on the mid-Atlantic ridge, and, given that Tunnicliffe *et al.* (1998) listed 443 hydrothermal vent species, dirivultids constitute over 10 percent of the faunal diversity at hydrothermal sites. They have been found in the washings of tubicolous polychaetes, gastropods, bivalves, and in the gill chambers and around the oral region of shrimps and crabs, as well as attached to the tentacular crown of vestimentiferan worms. Dirivultidae can be hyperabundant at vent sites as illustrated by Humes (1990b) who found over 15,000 individuals of *Stygiopontius quadrispinosus* Humes, 1987, in 210 ml of flocculent material collected at the Gorda Ridge in the Eastern Pacific. Of particular significance was Arthur's discovery of eight pairs in amplexus of this species which subsequently provided the first information on the functional morphology of the digeniculate antennules and their role in precopulatory mate guarding in siphonostomatoid copepods (Huys and Boxshall, 1991).

A second family of siphonostomatoid copepods, the Ecbathyriontidae, was established by Humes in 1987, based on a single new species found in the deep-sea hydrothermal vent fauna on the Galapagos Rift. This family remains monotypic and its host group is unknown. It is of particular phylogenetic interest in that, in addition to the large aesthetasc derived from ancestral antennulary segment XXI, the male of *Ecbathyrion prolixicauda* Humes, 1987, retains an exceptionally high number of aesthetascs, those derived from ancestral segments I to IV, VII, IX to XI, XIV, XVI, and XVIII (Huys and Boxshall, 1991).

Another hydrothermal vent family established by Humes, the Erebonasteridae, is the only family of the order Poecilostomatoida in which ventral copulatory pores are found that are separate from the genital apertures on the dorsal surface of the female genital double-somite. It is also the only family in the order to retain a discrete mandibular palp (Humes, 1987). The family is characterised by these two extreme plesiomorphic states and this family, together with another family—the Fratiidae (cf. Ho *et al.*, 1998)—of invertebrate associates, will be of pivotal importance in the emerging concept of the Cyclopoida

and Poecilostomatoida as a monophyletic taxon.

His Legacy

In this short appreciation we cannot do justice to the breadth and depth of Arthur Humes's contributions to copepod taxonomy. We have attempted to pick out a few highlights that seem, to us, to be of particular significance. We wish to stress that the accuracy and detail of Arthur Humes's taxonomic descriptions and those of his students, Roger Cressey, Richard Gooding, Ju-shey Ho, and Masahiro Dojiri, are exemplary. He set a consistently high standard in his illustrations, which ensured he was providing data that would be of lasting value in biodiversity studies and phylogenetic analyses long into the future. His students continued this tradition, and Arthur's far-reaching influence will be of benefit to copepodology far into the 21st Century.

Arthur was a born systematist who loved to synthesize information. His synoptic treatments made it possible to become familiar with the wide diversity of copepods associated with particular host groups such as the Holothuroidea (Humes, 1980), Actiniaria (Humes, 1982a), Asteroidea (Humes, 1986b), and Alcyonacea (Humes, 1990a), and to identify them without having to possess the scattered original literature. Arthur always went to great effort to identify the host in order to promote studies on host specificity and geographical distribution. He believed that knowledge of the exact host name could potentially shortcut the identification process significantly, and therefore he regularly updated records on host-copepod associations in a synthetic cross-referenced format.

From the start of his career Humes recognized that name-bearing types are the sole international standards of reference and should be deposited in an institution that maintains a research collection with proper facilities for preserving them and making them available for study to others. More than just being a tireless collector, Arthur deposited type material of each of the 700+ species he described in international museums such as the National Museum of Natural History in Washington, the Natural History Museum in London, the Rijksmuseum van Natuurlijke Historie in Leiden, the Zoölogisch Museum in Amsterdam and the Muséum National d'Histoire Naturelle in Paris. His collections frequently comprised hundreds of paratypes of which he would normally deposit the vast majority in a major museum and the remainder in his own wonderfully arranged reference collection. In addition, he deposited material of numerous other species, previously described by others but rediscovered during his own fieldwork. His meticulously curated personal collection was bequeathed to the National Museum of Natural History and together with his earlier donations constitutes the largest copepod collection accumulated ever during an individual's lifetime. The new fourth edition of the International Code of Zoological Nomenclature has introduced a mandatory requirement for the availability of new species-group taxa published after 1999, i.e., a statement naming the collection in which the type is or will be deposited (Art. 16.4.2). As with his methods Humes was well ahead of his time and ensured a lasting legacy.

Arthur undoubtedly left many works unfinished. The fact that interest in the siphonostomatoids did not equal interest in the poecilostomatoids is largely due to Arthur's influence and contribution. On several occasions he referred to the many collections of siphonostomatoid copepods, acquired during his nearly four years of fieldwork in the 1960s and 1970s, and still awaiting study in his lab. Similarly, he felt that his collections of copepods associated with ascidian hosts had not yet received the attention they deserved. During the Fifth International Copepod Conference in Baltimore in 1993, the last of its kind he attended, Arthur voiced his intention to continue describing copepods until the turn of the millennium. In view of Arthur's sustained output in recent years, which showed no sign of decline, and the prospect of more research time following his retirement as Editor of *Journal of Crustacean Biology*, it is unlikely that this turning point would have marked the end of his extraordinarily productive career.

In recognition of his monumental work on copepod systematics Arthur Humes was a recipient of the Research Excellence Award given by The Crustacean Society. Uniquely, the Board of The Crustacean Society voted to bestow this honour on Arthur Humes posthumously, since the nomination process had been completed before his death. At the win-

ter meeting of The Crustacean Society in Atlanta in January 2000, the award was presented by the President, Dr. Joel Martin, to Dr. Charles Derby who accepted it on behalf of Arthur Humes. This award has since been renamed the Arthur G. Humes Award for Research Excellence.

It is difficult to imagine the field of associated copepods without Arthur Humes. In these times of decreasing support for, and interest in, taxonomic research, the shear volume of his work may never be surpassed. To paraphrase the title of his own past-presidential address presented at the Annual Meeting of the American Microscopical Society in Denver in December 1984 (Humes, 1985b), any biographical sketch of the man, who never lost his fascination with his beloved animals, could simply be condensed as "Arthur Humes and Copepods: A Success Story."

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