

PROTO- ARTHOPODS DIVERSITY, ESSENTIAL FOR UNDERSTANDING

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ABSTRACT

Arthropods constitute a central and colossal component of Earth's biosphere, at both the macroscopic and microscopic levels. Since the beginning of the Phanerozoic, these hyperdiverse, articulated animals have shaped most terrestrial and marine ecosystems, and their pivotal roles in trophic networks often have a direct and considerable impact on our industries and economy—be it vital or detrimental. The war on insects, prominently, waged in the name of a wasteful and profit-driven agriculture, has led to catastrophic consequences for the survivability of these animals worldwide, and the loss of pollinators to cascading ecosystem breakdowns. The agro-economical peril to arthropods, in conjunction with other environmental crises caused by unbridled resource exploitation and consumption, such as global warming, threatens to irremediably pauperize the planet's landscapes. This waning and fragility stand in stark contrast to more than half-a-billion years of exceptional resilience to mass extinctions. Although trilobites, vanishing at the end of the Permian, are a notable exception, the body plans (which can be broadly defined based on morphoanatomy, see e.g. Aria of all other four largest and traditional arthropod groups—chelicerates, myriapods, “crustaceans” and insects—, all present by at least by the Late Devonian, diversified through all of the five major preAnthropocene biodiversity crises. Likely since the Jurassic insects have become by a large margin the most diversified and abundant of arthropods but all main lineages have characteristically experienced explosive radiations and have shown extended stability of their families and genera.

Keywords: Proto- Arthropods, Diversity

INTRODUCTION

Arthropods constitute a central and colossal component of Earth's biosphere, at both the macroscopic and microscopic levels. Since the beginning of the Phanerozoic, these hyperdiverse, articulated animals have shaped most terrestrial and marine ecosystems, and their pivotal roles in trophic networks often have a direct and considerable impact on our industries and economy—be it vital or detrimental. The war on insects, prominently, waged in the name of a wasteful and profit-driven agriculture, has led to catastrophic consequences for the survivability of these animals worldwide, and the loss of pollinators to cascading ecosystem breakdowns. The agro-economical peril to arthropods, in conjunction with other environmental crises caused by unbridled resource exploitation and consumption, such as global warming, threatens to irremediably pauperize the planet's landscapes. This waning and fragility stand in stark contrast to more than half-a-billion years of exceptional resilience to mass extinctions. Although trilobites, vanishing at the end of the Permian, are a notable exception, the body plans (which can be broadly defined based on morphoanatomy, see e.g. Aria of all other four largest and traditional arthropod groups—chelicerates, myriapods, “crustaceans” and insects—, all present by at least by the Late Devonian, diversified through all of the five major

preAnthropocene biodiversity crises. Likely since the Jurassic insects have become by a large margin the most diversified and abundant of arthropods but all main lineages have characteristically experienced explosive radiations and have shown extended stability of their families and genera. The search for the causes and mechanisms surrounding the origin of the highly modular architecture that has been certainly determinant in the success and expansion of the arthropod phylum has therefore focused on the earliest Phanerozoic, and specifically the Cambrian explosion. Starting with the Burgess Shale, a variety of Cambrian Fossil Lagerstätten across the world have yielded a wealth of nonbiomineralizing species informing early diversity and character transitions leading to arthropods and to their ramifications. In this context, arthropods have famously initiated discussions about shifts in evolutionary tempo and mode at the macroevolutionary scale (that is, at the inter-specific taxonomic level and above and in particular the heterogeneity of disparity patterns and their possible meaning for body plan evolution). The insights and developments following these studies have been marked by debates about the deep phylogenetic relationships between arthropods, to which fossil taxa contributed in increasingly significant ways in the context of a still seemingly intractable phylogeny of extant lineages. In the last ten years, broad-scale combined morphological and molecular phylogenetics and phylogenomics have broken the systematic deadlock by achieving strong branch support and topological convergence for major extant clades even if the resolution of certain internal nodes remains a salient issue. There is now robust evidence that all extant arthropods can be divided into two main lineages:

CHELICERATA AND MANDIBULATA

the latter including Myriapoda as well as Pancrustacea (also called Tetraconata), a broad grouping according to which Hexapoda (including insects) arose from a paraphyletic crustacean group. The inclusion of fossils to one of these total-evidence datasets—key to a contextualized macroevolutionary perspective—has been shown to be consistent with these topologies. While summarizing certain solid advances in this field, this result did not mean, however, that the palaeontological understanding itself was complete, and recent findings, catalysed in part by the discovery of new fossil sites or the use of new technologies have since rewritten the significance of many extinct taxa. This, in turn, has changed our perspective on early body plan evolution in these animals, introducing new fundamental questions to current research. Conversely, a series of exceptional discoveries involving preserved neural tissues have lately been followed by broad scenarios describing the evolution of arthropod heads. However, some of these challenging new data have arguably been overinterpreted, emphasizing the importance of maintaining consistency with the information provided by external morphology. Beyond genes and morphoanatomy, an integrated palaeobiological and palaeoecological picture and its role in the early radiation of arthropods is also starting to take shape. We certainly are at a decisive turn where converge an unprecedented amount of often seemingly conflicting evidence from revised fossils, new fossils, new types of preserved tissues, genes, development, genetic networks, new technologies, and new phylogenetic methods. This review aims to provide a simple but critical guide to current knowledge, and to lay out a synthesis of persisting or emerging challenges in early arthropod evolution, to serve as foundation for future studies. The stakes are high, for the elucidation of the early diversification of the largest animal phylum may also provide the richest insight into the biological principles governing macroevolution. The panarthropod cradle and a “Cambrian planktonic revolution” Arthropoda is now recognized as a monophyletic phylum within Ecdysozoa, the moulting animals.

PRESENCE OF A PERITROPHIC MEMBRANE OR MALPIGHIAN TUBULES

A recent fossil-inclusive analysis found Tardigrada to be the sister group to Onychophora + Arthropoda consistent with most other phylogenetic studies. This result is influenced by the fact that, in spite of their dramatic developmental contraction, tardigrades display the plesiomorphic condition of a truncated posterior termination bearing a limb pair with claws pointing anteriorly—possibly inherited from the pool of adaptations acquired by suspension-feeding lobopodians, which includes an anchoring function of posterior lobopods. The plesiomorphic presence of more trunk somites and the presence of several elongate, curved claws on their limbs are consistent with a sister-group relationship with the Burgess Shale lobopodian *Aysheaia pedunculata*. However, while providing detailed genetic and phenotypic information, tardigrades and onychophorans are also typified by a number of outstandingly autapomorphic characters (onychophorans appear to have independently evolved a ventral mouth opening and internalized mouthparts and, like many tardigrades, are largely terrestrial), which urges caution when attempting to extrapolate shared derived conditions. By contrast, fossils called lobopodians, mostly found in Cambrian rocks, have directly enriched our understanding of the early evolution of panarthropods. Although specimens are characteristically rare across assemblages, these worm-like taxa bearing paired metameric, annulated and lightly sclerotized limbs (the lobopods) have revealed that a broad diversity of organisms had in fact initially evolved from cycloneuralian ancestors. Fossil-inclusive phylogenetic analyses find tardigrades to be well nested within Panarthropoda, and show that the surviving Onychophora and Tardigrada are, indeed, but offshoots with highly autapomorphic traits from this initial radiation associated with the Cambrian explosion. Other lobopodians survived through the Silurian up to at least the Carboniferous however, which means that they represented much more than an “experimental” body plan and had eventually reached a relatively stable (if cryptic) adaptive zone within Palaeozoic marine ecosystems. Perhaps the most important aspect of lobopodians put forward in the recent years is their arguably common adaptation, at various degrees, to suspension-feeding. Most striking among the Luolishaniids, which possess stout anchoring back limbs and frontal arms adorned with pairs of thin spinules, this ecology also possibly characterizes the famed Hallucigeniids and would thereby apply to a majority of lobopodians with diagnostically elongate appendages. These are distinct from a series of other taxa, including much larger and stouter forms (termed herein ‘xenusiids’), that bear short and conical lobopods, as they are known in onychophorans and tardigrades, and which would lie closer to the common arthropod ancestor. Whether arthropods and their closest relatives arose from a paraphyletic lineage of suspension-feeders or whether suspension-feeding triggered a separate, monophyletic radiation depends on the evolutionary scenario considered but it appears that the distinction between an ambulatory or semi-sessile feeding lifestyle was determinant in the primordial diversification of panarthropods. Parallel studies on the first arthropods, the radiodontans (I use here a definition of Arthropoda based on the presence of an arthrodized appendage see also Box, add even greater significance to suspension-feeding, broadly defined, in the rise of this phylum. A filter-feeding strategy, more precisely (which uses a filtration structure and captures food particles below a precise size threshold as indeed been shown to be present in several relatives of the iconic predator *Anomalocaris*, having evolved multiple times within the group and led to gigantism in the Ordovician. Contrary to long-legged lobopodians, however, filter-feeding in radiodontans was entirely carried out by the extensive modification of a single pair of appendages—the frontal, arthrodized appendages, characteristic of this group which otherwise lacks any body or limb arthrodization.

These appendages are coined here “cheirae”. This evidence further emphasizes the central role of small macro- to microscopic organisms in Cambrian sea waters, and notably larvae. It should be in fact questioned whether

the “planktonic revolution” thought to characterize the Great Ordovician Biodiversification Event] should not be placed within the Cambrian instead, correlated to a massive and sudden expansion of suspension-feeding strategies born during the Ediacaran Cases of suspension-feeding cited above among Cambrian panarthropods have been expanded to more derived fossil taxa and thoroughly spread across all Metazoa, in sponges, cnidarian polyps, echinoderms, brachiopods and a variety of other animals. Certain localities, like Marble Canyon, were arguably even built on suspension-feeding. Although the fossil evidence for small meso- to microplankton is still largely indirect. Small Carbonaceous Fossils (SCFs) and “Orsten” taxa from different localities around the world directly document the existence of abundant, planktonic crustaceomorph faunas that may be related to known mandibulate macrofossils (see below). Burgess Shale-type (BST) deposits do not preserve well micrometric fossils simply because of grain resolution limit, but there is plentiful evidence of tiny arthropod-like fossils, which, for the most part, are undescribable (pers. obs.), although several post-hatchling stage larvae have already been published some of them differing somewhat in morphology from their adult counterparts, pointing to ontogenetic niche differences. Arthropods being already the most diverse and abundant of animals by the early Cambrian, their larvae must therefore have constituted an important part of planktonic life forms, even if there were plenty of benthic direct developers. Radiodontans, nonetheless, also developed a much broader diversity of specializations involving the cheirae of radiodontans, which also includes sediment sifting for instance. Similar observations can be made about the variety of shapes realized by other arthropodized limbs and arthropod body segments, by comparison with the rather conservative morphology of lobopodians. Arthropodization, as a structural innovation, was therefore decisive in the early success of arthropods by providing a modular medium with both developmental flexibility and structural rigidity, a “sculpting material” that worked particularly.

(Previous page) Variety of preservations and fossils that have recently reshaped or challenged our views on early arthropod evolution. a, *Alacaris multinoda* Yang et al. specimen YKLP 12268 (holotype), from the Xiaoshiba biota; a fuxianhuiid. Image courtesy of Xiguang Zhang. b, *Ercaicunia multinodosa* Zhai et al. specimen YKLP 16201, from the Chengjiang biota; a hymenocarine. X-ray computed tomography, image courtesy of Dayou Zhai. c, *Mollisonia plenovenatrix* Aria and Caron specimen ROMIP 65262, from the Burgess Shale (Marble Canyon); an early chelicerate. Image courtesy of Jean-Bernard Caron. d, *Gnathobasis* of *Wisangocaris barbarahardya* Jago et al. specimen SAM P45629, from the Emu Bay Shale; a habeliid. Image courtesy of Jim Jago. e, *Yicaris dianensis* Zhang et al. specimen YKLP 10844, from the Yu’an shan “Orsten” biota; a larval crustaceomorph. Scanning electron microscopy, image courtesy of Xiguang Zhang. f, *Surusicaris elegans* Aria and Caron specimen ROMIP 62976 (holotype), from the Burgess Shale (Marble Canyon); an isoxyid. Image courtesy of Jean-Bernard Caron. g, *Kerygmachela kiera* Budd specimen MGUH 32048a, from Sirius Passet; a swimming lobopodian. Image courtesy of Jakob Vinther. h, i, *Aegirocassis benmoulae* Van Roy et al. from the Fezouata biota; a radiodontan. Images courtesy of Derek Briggs. h, Specimen YPM 527123, filter-feeding frontal appendages. i, Specimen YPM 237172, whole body, three-dimensional. j, *Cascolus ravitus* Siveter et al. specimen OUMNH C.29698, from the Herefordshire biota; a possible malacostracan. Digital reconstruction from serial photography, image courtesy of David Siveter, Derek Briggs, Derek Siveter, Mark Sutton and David Legg. k, *Hongshiyana spisyiliangensis* Zhang and Lin in Zhang et al. specimen NIGPAS 164503, from the Xiazhuang biota; a trilobite. Image courtesy of Han Zheng. l, *Ovatiovermis cribratus* Caron and Aria], specimen ROMIP 52707, from the Burgess Shale (Walcott Quarry); a suspension-feeding lobopodian. Image courtesy of Jean-Bernard Caron. m, *Yawunikootenayi* Aria et al. specimen ROMIP 63066, from the Burgess Shale (Marble Canyon); a lea choiliid megacheiran. Image courtesy of Jean-Bernard Caron. Arrowheads point to: subdivided, enditic basipod (a), raptorial and sensory

complex of appendages (c), tripartite exopods (k), stout lobopods for anchoring (l) and robust basis of cheira (m). Abbreviations: an, antennule(s); at, antenna(e); ca, carapace; cr, cheira(e); cs, cephalic shield; en, endopod(s); gn, gnathobasipod; he, h-element “carapace”; la, labrum; lb, lobopod(s); lbf, lobopodous flaps; le, lateral eye(s); ma, mandible(s); me, median eye(s); mo, mouth apparatus; mp, mandibular palp; mx, maxillula and maxilla; ph, periintestinalhemocoelic cavity; py, pygidium; ta, trunk appendage(s). Scale bars, 10mm (a, g, m), 1mm (b, j), 3mm (c, f, k, l), 2mm (d), 100µm (e), 20mm (h), 100mm (i). well as a rapid driver of phenotypic evolution, notwithstanding the anatomical and genetic trade-offs that later stabilized a number of well-defined body plans. Assembly of the arthropod body plan One of the most interesting and well-documented sequences of phenotypic evolution from cycloneuralians to arthropods is that of the mouth and its associated structures.

Some basal lobopodians possessed an eversible pharynx lined with teeth, similar to that of priapulids others, like *Hallucigenia*, had also independently evolved circumoral sclerotic plates reminiscent of radiodontans (but expressed internally). The dented pharynx is a plesiomorphy of arthropods, and has been retained by extant taxa. The location of the mouth was terminal from cycloneuralians through xenusiids however, the first midgut glands only appear in xenusiids suggesting an evolution in the mode of feeding and/or diet in these animals, possibly associated with the introduction of predation or irregular scavenging From a xenusiid-like ancestor emerged peculiar lobopodians, such as *Kerygmachela* and *Pambdelurion* (long endemic to the early Cambrian Greenland locality of Sirius Passet, but possibly present elsewhere), apparently bearing flap-like swimming appendages, in addition to lobopods. By contrast to xenusiid ancestors, *Pambdelurion* displays a circumoral sclerotic mouth apparatus clearly placed on the ventral side of the body, although it was argued that the animal also retained an eversible pharynx The rotation of the mouth opening, which in extant lineages is characteristically ventral with posteroventral orientation and connected to an anteriorly-looped esophagus, therefore occurred during the xenusiid-radiodontan transition *Kerygmachela* may document a transitional morphological state in which the mouth opening is ventral but directed anteriorly A circumoral sclerotized apparatus, giving its name to radiodontans (radius (Latin) – *odoús* (Greek) meaning literally radial-teeth), exemplified by *Anomalocaris* or *Hurdia* is therefore not exclusive to this group. A ‘peytoia’ type of outer sclerotized ring (or its derivatives composed of differentiated plates (by their size), also commonly called the “oral cone”, would unite radiodontans, but resemblances with *Pambdelurion* are extensive, to the point that some isolated radiodontan-like mouthparts from the Chengjiang biota were proposed to belong to a relative of *Pambdelurion* The numerous inner teeth of *Pambdelurion* are found in radiodontans in the form of an inner row of smaller dented plates, which could be derived from the symplesiomorphic pharyngeal teeth. Interestingly, a comparable set of elements are also found in dissociation in amplexobeluid radiodontans from the Chengjiang biota, never forming the typical oral cone.

REVIWE OF LITRATURE

Islam, M.S., Roy, B.K., Rahman, M.A., and Islam, M.N. (2013). Water Quality Assessment of Ghurdaur Pond of Rajshahi University, Bangladesh. *Journal of Environmental Science and Natural Resources*, 6(1): 87-92. This study conducted an assessment of water quality parameters such as pH, dissolved oxygen, turbidity, and nutrient concentrations in Ghurdaur Pond and identified potential sources of pollution.

Khan, S.A., Ahmed, M., Ahmed, S., and Ahmed, Z. (2016). Ichthyofaunal diversity of Ghurdaur Pond, Rajshahi University campus, Bangladesh. *International Journal of Fisheries and Aquatic Studies*, 4(2): 452-

456. This study documented the diversity of fish species in Ghurdaur Pond and identified potential threats to the fish population.

Barua, A., and Rashid, H. (2018). Limnological studies of a freshwater pond at Sylhet Agricultural University, Bangladesh. *International Journal of Fisheries and Aquatic Studies*, 6(6): 369-374. This study conducted a limnological analysis of a freshwater pond in Bangladesh and provided insights into the physical and chemical characteristics of the pond.

Haque, M.A., Rahman, M.A., Hossain, M.S., and Islam, M.R. (2020). Water Quality and Trophic State of Ghurdaur Pond, Bangladesh. *Journal of Environmental Science and Natural Resources*, 13(2): 25-30. This study assessed the trophic state of Ghurdaur Pond and identified factors contributing to eutrophication.

Islam, S.M.R., Islam, M.S., and Hasan, M.R. (2021). Fishing and Livelihood Pattern of Local People Around Ghurdaur Pond, Bangladesh. *Journal of Fisheries*, 9(2): 612-619. This study examined the fishing practices and livelihood patterns of local communities around Ghurdaur Pond and identified opportunities for sustainable resource management.

"Mammalogy: Adaptation, Diversity, Ecology" (2019) by George A. Feldhamer, Lee C. Drickamer, Stephen H. Vessey, Joseph F. Merritt, and Carey Krajewski. This textbook provides an overview of the biology, evolution, and ecology of mammals, including their classification, anatomy, physiology, and behavior. The authors cover topics such as mammalian adaptations to different environments, reproductive strategies, and conservation.

Research Methodology

Spectroscopy and its applications form a significant part of modern Chemistry, Physics and Biology. From its derivation, the word spectroscopy appears to mean the watching of images but the modern subject covers the interaction of electromagnetic radiations with matter. The most important consequence of such interaction is that energy is absorbed or emitted by the matter in discrete amounts called quanta. The absorption or emission processes are known throughout the electromagnetic spectrum ranging from the gamma region (nuclear resonance absorption or the Mossbauer effect) to the radio region (nuclear magnetic resonance). When the measurement of radiation frequency is done experimentally, it gives a value for the change of energy involved and from this one may draw the conclusion about the set of possible discrete energy levels of the matter.

Electron Spin Resonance in Copper Protein Studies: ESR is a non-destructive spectroscopic technique of which transitions between the Zeeman levels, with the absorption of energy, may be observed when compounds with unpaired electrons (Paramagnetic metal ions, free radicals, triplet states) are placed in a magnetic field. Cupric copper, Cu (II), has one unpaired electron, is paramagnetic and gives an ESR absorption. Cuprous copper, Cu (I), is diamagnetic and cannot be observed by ESR.

The quantities experimentally measured from ESR spectra of Cu (II) compounds are the g-values, the hyperfine splitting constants and the area under the absorption curve. The g-values (dimensionless numbers) and hyperfine splitting constants (expressed in gauss or Cm^{-1}) related to the symmetry of the arrangement of the ligand atoms about the Cu (II) ion and to the covalency of the Cu (II)-ligand bonds; the area under the absorption curve measures the total amount of Cu (II).

The two naturally occurring copper isotopes, Cu and ⁶⁵Cu, have nearly identical magnetic moments and each has a nuclear spin of 3/2. The ESR absorption is therefore split into four absorption peaks called the hyperfine structure (hfs). This hfs consists of four equally spaced symmetric absorption peaks for each set of equivalent Cu (II) sites in a single crystal (Kokoszka, 1967). The separation between the adjacent peaks is 'A', the hyperfine splitting constant. When the orientation of the single crystal is changed with

respect to the external magnetic field, the field strength at which absorption occurs changes since the g-value is generally anisotropic. The g-values of Cu (II) complexes are usually axially symmetric which reflects the axial of the Cu (II) site. g is measured with the applied field in the plane perpendicular to the axis and g_{||}, with the field applied along the axis. It is possible, in principle, to determine the g-values from ESR absorption curve obtained with randomly oriented samples. This was first shown by Bleaney (1951) and has been extended by others (Sands, 1955). The g-values and the A-values can not be determined accurately by simple inspection, however, because the absorption lines overlap and the total absorption curve is no longer symmetric.

Theoretical ESR absorption curves for randomly oriented Cu (II) complexes have been calculated by assuming a specific symmetry of the Cu (II) site. Fig. 1 is a calculated absorption curve for Cu (II) in a site of axial symmetry assuming infinitely narrow lines (Sands, 1955). The two g-values g_⊥ and g_{||} are located in the positions shown in Fig. 2. When the four hyperfine absorption curves are summed and differentiated (now assuming a finite line width), the first derivative spectrum results. This is shown in Fig. 2, as given by Aasa et al., (1964). To accurately determine the g- and A-values, theoretically calculated spectra are fit to the experimentally determined absorption curves.

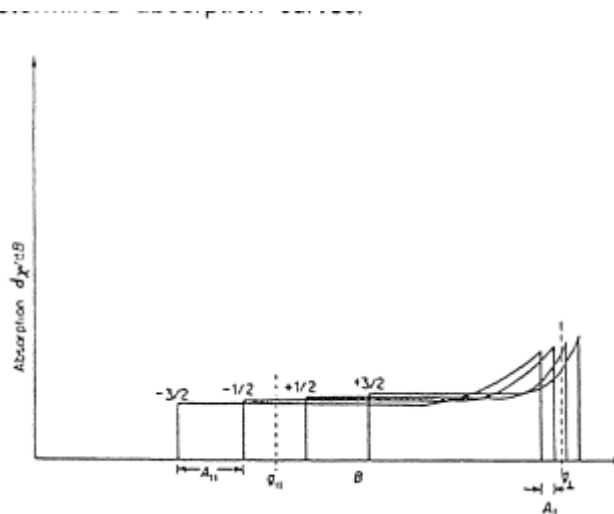


Fig 1 Calculated hyperfine ESR absorption curves for Cu(II) in a site of axial symmetry in a sample with random orientation of the Cu(II) sites. The line width was assumed to be infinitely small (after Sands 1955). The absorption of microwave energy, dy/dB , is plotted against the field strength, B . The g-values are calculated from $g = hv/\beta B$. The numbers $-3/2, -1/2, 1/2$ and $3/2$ represent the four allowed orientations of the nuclear magnetic moment associated with a given absorption curve. Empirically, the curves do not exhibit discontinuities at the high and low field ends of the spectrum because the line width is finite.

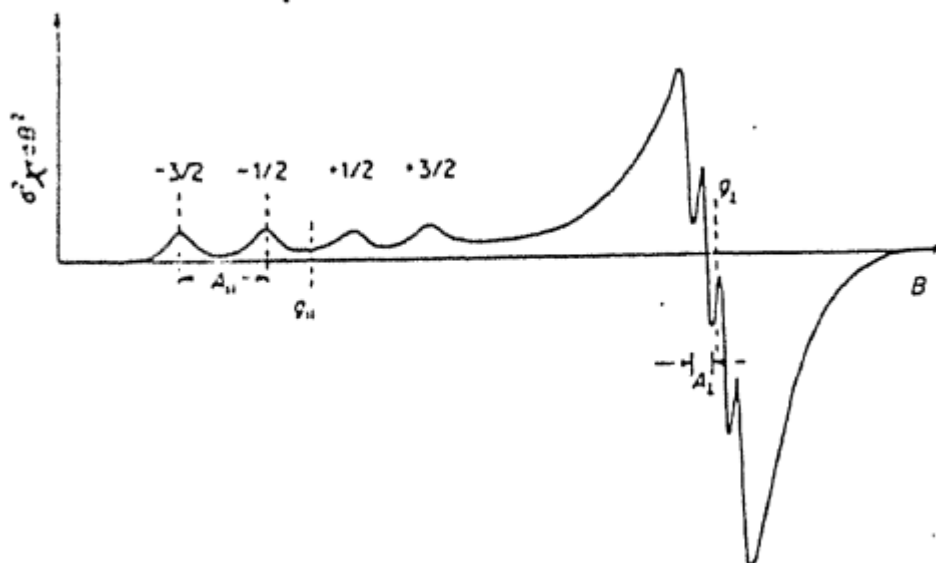


Fig 2. First derivative of the ESR absorption curve given in Fig. 2. This is the way in which experimentally determined ESR spectra are presented. The quantities g_1 , Δ_1 and A_{11} are measured as shown in the figure. Frequently, due to small A_{11} values and large line widths, the hfs in the g-region cannot be resolved,

CONCLUSION

Hemocyanin is a copper containing respiratory pigment present in some of the members of Arthropoda and Mollusca. This blood pigment combines reversibly with molecular oxygen and mainly functions in the transport of oxygen. The copper and protein contents are more in the scorpion hemolymph than crab and snail. It is due to high hemocyanin concentration in the blood of the scorpion which can be correlated with the terrestrial life. The per cent copper recorded for crab scorpion and snail native hemocyanin are 0.168, 0.170 and 0.258 and that for apohaemocyanins of crab, scorpion and snail are 0.012, 0.015 and 0.046 respectively. For the first time apohaemocyanin was prepared out of native hemocyanin. Nearly 96 per cent of copper was removed from crab and scorpion hemocyanin by treatment with cyanide. Whereas not more than 81 per cent of copper could be removed from the snail hemocyanin. The maximum absorption bands of the oxyhaemocyanin of crab, scorpion and snail studied are found to be at 580, 580 and 575 nm respectively. The optical density values of the oxyhaemocyanin of the scorpion is more than the crab and snail suggesting higher concentration of hemocyanin in the scorpion.

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