

# OBITUARY

*Cladistics* (1993) 9:357–367

## LARS BRUNDIN

30 May 1907–17 November 1993



Professor Lars Brundin, of Stockholm, Honorary Fellow of the Willi Hennig Society, died in November 1993 at the age of 86. A pioneer of cladistics Lars encountered the ideas of Willi Hennig in the 1950s. He immediately realized their great importance for biology and made them central in his own pioneering research on the biogeography of the southern continents and thereby played a pivotal role in the emergence of phylogenetic systematics. Much of the later developments in cladistics can be traced back to the influence of Lars Brundin. He did not himself give birth to cladistics, but if anything, he was the doctor who brought forth the baby, gave it a healthy start in the world, and announced the event to a reluctant scientific community.

To those of us, who studied biology in the 1960s, systematics appeared to be a dull, almost dead subject. Brundin, enthusiastic and lucid on “vicariance”, “Hennig’s principle” and the “search for the sister group”, came like a gust of fresh air blowing through a stale room. We will miss his clear intellect, his crisp comments and the dense clouds of pipe smoke that used to cover those debates in which he was an integral part until what seems just recently. That is all gone: “When a man dies it is like a library burning down to the ground. All is lost”. Rather than expanding on his merits, let us give the word to Lars Brundin himself for one last time. This manuscript shows how he looked upon his achievements.

## FROM GRIMSGÖL TO GONDWANALAND—HALF A CENTURY WITH CHIRONOMIDS

**Lars Brundin<sup>1</sup>**

My interest in Chironomid midges was not awakened until relatively late in life. My father was a senior master of biology at the high school of Växjö, an experienced field botanist and entomologist, specialising in Lepidoptera. During our school time excursions in the Smolandic neighbourhood, I devoted myself enthusiastically to the study of beetles, using the efficient sieve method which resulted in the discovery of several rarities. These summer holidays of my school time, dedicated to field work and identification of species by means of the literature available, sharpened my eye for morphological details and the ecological differences between the species, and this in turn led to an increased understanding of the boundaries between species and of individual variation.

This experience was a great asset when I, after graduating from the high school of Växjö in the autumn of 1925, began my science studies at the University of Lund, specializing in entomology. An event of great importance occurred in spring 1927, when I was asked by my teacher of entomology, the "docent" Simon Bengtsson, on the initiative of professor Yngve Sjöstedt at the Natural History Museum in Stockholm, if I wanted to initialize a survey of the insect fauna of the Abisko National Park. There was no doubt about the answer, of course, and during two summers I collected Coleoptera and Lepidoptera in that mountain area, so richly endowed by nature. The result of this survey was published in the conservation series of the Royal Academy of Sciences. In Abisko, however, I had met several of the leading Swedish botanists and through them discovered plant sociology, a theme very popular at the time. Its foundations had been laid mainly by studies of the vegetation of the Scandinavian mountains, nearly unaffected by man. This led to a detailed investigation of the qualitative and as quantitative distribution of insects within the most important, clearly-defined plant societies of the birch region, as well as of the tree-less Arctic region using the numerous Coleoptera as indicators. The result was a thesis titled "Die Coleopteren des Torneträskgebietes. Ein Beitrag zur Ökologie und Geschichte der Käferwelt in Schwedisch-Lappland" (Brundin, 1934). The reception was middling, partly, maybe, because the topic was new. I, myself, was also fairly green at that time, I suppose.

After the defence of my thesis I became engrossed in taxonomic studies in the largest Coleopteran genus *Atheta*, belonging to the Staphylinids, commonly considered the most difficult of the Coleopteran groups. Until then, I had been totally dependent on specialists and I felt this as a challenge. Due to an improved method for the preparation of the genitalia the progress was swift. A number of revisions of the Palaearctic species belonging to different *Atheta* groups, including many new species, were the result, the latest appearing in 1953.

### **The Chironomids of Swedish Lakes as Ecological Indicators**

The above was my background when a drastic change took place in 1936. I received a scholarship at the Government Institute for Fresh Water Research at

<sup>1</sup> Probably originally written in 1985. Translated by H.-E. Wanntorp.

Drottningholm, near Stockholm, where I received an associate professorship the following year. Here I made my first contact with limnology, the causally-oriented, ecological freshwater research. During the preceding two decades, limnology had made swift progress, with Einar Naumann in Lund and August Thienemann in Plön as inspiring leaders. It was a lucky star that brought me to Drottningholm, and the 20 years at the laboratory under sympathetic professors like Gunnar Alm and Sven Runnström formed a period of dedicated research devoted to the bottom fauna of Swedish lakes and its dependence on various environmental factors. Naturally, it took time to work through the literature and form a general view of the various problems. I encountered Chironomids in 1936–1939, and especially their larvae, as a consequence of my duty to investigate the fish and bottom fauna of some lakes in northern Sweden. The result was presented in “Zur Limnologie jämtländischer Seen” (Brundin, 1942). For various reasons a more thorough discussion about the relationships between these lakes and the lake types of Thienemann was not possible.

At that time, limnologists commonly applied the concept of “larval types” of Chironomids with the optimistic notion that each larval type, though often representing more than one species, was ecologically homogeneous. This obviously led to confusion and mistaken generalizations. One also tended to neglect that Thienemann’s lake types were based on the profundal Chironomid fauna of permanently stratified lakes. Consequently a multitude of new lake types has been proposed from various parts of Europe, including Fennoscandia; all with profundal faunas differing from those of Thienemann’s classical types. Actually, the proposed types often represented lakes with unstable stratification and comparatively warm bottom water in the profundal zone. This allowed the invasion of more or less eurythermal elements from the littoral zone. These weaknesses were also inherent in those investigations of the bottom fauna which had been made in the lakes of the Aneboda area north of Växjö, classical since Naumann’s analyses of Algae and bottom sediments.

With this background, I decided to take on a major project, namely to investigate thoroughly the chironomid fauna of some of the lake types from the Aneboda–Växjö area and compare the result with samples from other parts of Sweden. The field work commenced in 1942. It included collecting with an “Ekman sampler” along certain bottom profiles during varying seasons, collecting of pupal skins on the surface, and of hatching pupae in funnel traps suspended over varying depths, net collecting of imagines in the shore vegetation, and hatching of imagines from fully-grown larvae. For type lakes I chose the permanently stratified, extremely polyhumous *Sphagnum* mere Grimsgöl, the permanently stratified polyhumous Lake Skärhultssjön, the meta-stably stratified somewhat humous Lake Stråken, the unstably stratified oligohumous Lake Innaren, and the permanently stratified oligohumous Lake Skären. This series of type lakes demonstrated the influence on the bottom fauna, qualitatively as well as quantitatively, of increasing humosity, and also the consequences of stratification on the qualitative aspect of the profundal fauna.

One strong point was that the causal analyses were based entirely on Chironomid material identified to the species level, another was that I had undertaken all the details of the investigation myself, in the field and in the laboratory. Most of all I enjoyed the little *Sphagnum* mere Grimsgöl with its brandy-coloured water. In spite

of its extremely poor Chironomid fauna (37 species compared with the 140 species of Lake Innaren!) it turned out to be characterized qualitatively by some species peculiar to polyhumous waters; among these an undescribed species of *Chironomus*, having larvae of the *plumosus* type, which had been sought for a long time (*C. tenuistylus* Brund.). These indicator species were also found on Lake Skärhultssjön. Of its kind, the Grimsgöl mere is undoubtedly an ideal type lake.

The generality of my conclusions were then tested on a great number of lakes in different parts of Sweden. After 7 years of work, the results were published in a rather hefty volume titled "Chironomiden und andere Bodentiere der süd-schwedischen Urgebirgsseen" (Brundin, 1949). Previously, a considerable number of species new to Sweden or to science were described (Brundin, 1947, 1948).

My studies on Chironomid material from the deep lakes of the province of Jämtland had suggested that at least the lower parts of their profundal zone represented an environment at considerably lower trophic level than that of the shallower lakes in southern Sweden. The dominating species was *Heterotrissocladius subpilosus*, an Orthoclaदिine, earlier reported from the deep bottom of Lake Vättern in southern Sweden. Additional investigations in 1952 and 1955 of lakes above the timberline in northern Lapland (Katterjaure) and on the Jotunheimen in Norway demonstrated that the profundal bottoms were totally dominated by the same species there, though in less dense populations. Accordingly, I found it relevant to introduce the concept of *Heterotrissocladius subpilosus* lakes tied to the concept of ultra-oligotrophy (Brundin, 1956b, 1958). I could later verify the existence of this type of lake right across the North American continent.

#### THE CHIRONOMIDS OF THE SOUTHERN CONTINENTS AS ECOLOGICAL AND BIOGEOGRAPHICAL INDICATORS

During my work on the Swedish lakes and their Chironomids, it occurred to me now and then that the lakes of the temperate parts of the southern continents offered totally unsolved problems with reference to their bottom fauna. What are the counterparts to those Chironomids that inhabit the profundal zone of our lakes? Nothing was known about this. Slowly, the plan to go there myself to try to find an answer matured. Above all, I wanted to visit the lake district of southern Chile, where a string of lakes reached up against the outliers of the Andes. The plan to launch a small expedition to the Chilean lake district gained momentum and after 3 years' efforts I managed to raise, from various funds, a sum large enough to support three people for about 10 months. Most of the time was to be devoted to the Chilean lakes, including a few on the Argentine side, the rest to some lakes of the high Andes of Peru. My fellow travellers were H. Löffler, of Vienna, a water chemist and an expert on zooplankton and K. Thomasson, of Uppsala, an expert on phytoplankton.

We left Gothenburg on a Johnson liner at the end of July 1953 with a lot of equipment, and on 1 September we reached Santiago de Chile. Due to formalities and the typical indolence of Latin America, it was only after 5 weeks that we were ready to start our old American military jeep towards the south and the lakes. The programme was completed in the main, in spite of often primitive conditions, which, however, were compensated for by the privilege of working in the beautiful Chilean lake district where imposing volcanic cones usually dominated the view.

The large and deep Chilean and Argentinean lakes turned out to be harmonically oligo-mesotrophic. The profundal bottoms were inhabited by few species, among them some species of *Tanytarsus*, one species of *Monodiamesa*, and a relative of *Sergentia*, all of them endemic, but still direct counterparts to the indicator species of northern lakes. A counterpart to *Heterotrissocladius* was, however, searched for in vain. In fact, the paucity of species was striking in the South Andean lakes. As to total species number they could not even compete with the Arctic Lake Katterjaure in northernmost Sweden, which contains about 60 species. Even more extreme were the high Andean lakes in Peru. Thus, Lake Rinconada north of Titicaca, at a very high altitude (3 km long, 22 m deep at an altitude of 4680 m), had a rich littoral vegetation but was inhabited by only three species of Chironomids. Among these was, to my surprise, a species of *Chironomus*, with larvae of the *plumosus* type that inhabited the profundal zone. From Lake Titicaca (altitude 3815 m) only nine species were recorded (Brundin, 1956b). The Chironomid fauna of the tropical high Andes seems to be very young.

What fascinated me most at my work with the Chironomids after my return home in the summer of 1954 was the material that had been collected more causally, by netting along running waters, especially in southern Chile and Argentina. With the evolutionary approach that I had begun to adopt at this time, I saw that here was a material of great phylogenetic interest, indicating that the running waters of South America were inhabited by a Chironomid fauna, far richer and of higher age than that of the lakes.

From now on my scientific activities took a new turn. Although the Andean streams cried for a thorough investigation, it was clear that first I had to get acquainted with the rheophilic Chironomid fauna of the northern continents, especially the large subfamily Orthoclaadiinae. In 1955 a large material was collected from Sweden and Norway. For the purpose I constructed nets that were fastened along the streams in order to collect the biological drift containing hatching Chironomids, as well as their pupae and pupal skins. These nets turned out to be extremely efficient and from then on they remained by standard equipment. At the same time the European genera of the Orthoclaadiinae were revised and diagnosed taking the imaginal stage into account. It turned out that the numerous and partly drastic incongruences between the imaginal genera and the larval and pupal genera recognized by Thienemann did not exist, and that the latter were relevant in the main, also, for the imaginal stage (Brundin, 1956a).

The next preparation for my second journey to South America was a trip by car through North America in April–September 1957: starting west through Canada to Vancouver Island, then south through the Cascade Range and Sierra Nevada and back east through the U.S. The field work was concentrated to the well-preserved wilderness of the vast national parks and other reserves. The observations during the preliminary investigation in 1957–1958 of the many samples from running waters of North America formed a very valuable background for the future investigations far south. Before my North American trip, I was awarded the professorship of entomology at the Natural History Museum in Stockholm.

The second journey to South America took place in the beginning of 1959 and was completely devoted to the sampling of mountain streams and other running waters in the Chilean lake district, in the province of Magallanes, in Tierra del Fuego, and in the Cordillera Real of Bolivia. The results far exceeded my expecta-

tions. The number of species was considerable, as was the number of new genera and species. Of great interest, for example, were the characteristic representatives of a new subfamily, the Aphroteniinae. A striking fact was that the subfamily Podomiinae, which plays such a subordinate role in the Northern Hemisphere, in the southern Andes vies with the Orthocleriinae as to species numbers.

In connection with my work on this new South American material, some ideas were formed that resulted in the co-operation with the limnologist Vida Stout in *Christchurch, New Zealand*. After receiving some so-called Brunelin nets, she kindly collected samples in a number of streams on the South Island and sent them to me. My enthusiasm was great when I found in them representatives of several of those endemic groups that I then only knew from South America.

Thus, I came up against one of the key problems of biogeography. Maybe the most important of all, as an overall view of the history of life since middle Mesozoicum, depends strongly on the explanation given to southern connections: the fact that the southern part of the southern continents are inhabited by numerous animal and plant groups, which seem to be more closely related to each other (and to those of continental New Zealand) than to any group on the northern continents.

In the 1950s opinions were still much divided. Most biogeographers seem to have underestimated the age of the actual groups and started from the assumption of an unchanging map. They sought the explanation in the southward migrations from centres of origin in the northern continents, possibly in conjunction with secondary haphazard dispersals across the vast southern seas. Others preferred explanations involving large-scale geographical changes including former inter-continental land bridges. Very few considered Wegener's theory of continental drift and the former existence of a large southern continental block, *Gondwanaland*, that included all the southern continents, and later fragmented, thereby causing continuous biotic areas to split, giving rise to the patterns of vicariance that had fascinated biogeographers since Hooker and Wallace.

These earlier biogeographic discussions were clearly deficient in their lack of any convincing phylogenetic arguments. A biogeographer must always work with monophyletic groups and try to establish the degree of relationship between vicariating subgroups within any larger such group. At that time these requirements had not been satisfied in the attempts at analysing biogeographic problems. But, fortunately, the method was there to hand when I needed it, succinctly laid down in a treatise by Willi Hennig (Hennig, 1950), with complementary additions in a couple of papers (Hennig, 1953, 1957).

Hennig's epoch-making ideas went largely unnoticed for several years, but for my part there was no doubt that I had found the tool necessary for a successful analysis of the history behind the Antarctic vicariance pattern. Chironomids also seemed to be especially suitable for a phylogenetic analysis, since they belong to the holometabolous insects and their imagines, pupae and larvae all have different sets of morphological traits that may be tested against each other.

The project that I now planned, however, required a considerable amount of further field work. Due to favourable circumstances, I was able to visit Tahiti, New Caledonia, New Zealand, Tasmania, New South Wales and southern Queensland in 1961. On the way home, I also got the opportunity to place my nets in the mountain stream of the deep valleys below Darjeeling which brought melting water from

Kanchenjunga in order to check if my "Antarctic" groups could be traced in the eastern Himalayas. Finally, in 1963, I went to South Africa where samples were taken in the mountain streams along the south coast, especially in the few vestiges of original forests that still remain. The very last samples were collected on the slopes of the Drakensberg Mountains verging on the Indian Ocean. The journey to South Africa was well worth the effort, and, I noted in the field, some extremely important gaps in the overall picture were being filled.

A very rich Chironomid material had now been collected. The analysis had been going on between the trips, but in 1961 it became clear to me that my lifetime would not be sufficient for a full treatment. I thus decided to exclude the difficult subfamilies Orthoclaadiinae and Chironominae and concentrate my final work on three subfamilies, the Podonominae, Aphroteniinae, and Diamesinae; three monophyletic groups, evidently of southern origin and therefore of special interest.

Detritus collected in the stream nets with Chironomid material included was brought home, preserved in plastic jars with formalin solution. The extraction of the insects under the preparation microscope took its share of time, of course, but could not be left to anybody else, since a selection was always necessary due to the great number of specimens. But at the same time the work was thrilling and filled with interesting surprises.

Once all the necessary descriptions and figures had been finished (80% of the species were new), I could begin the phylogenetic analysis based on the comparative morphological survey thus obtained. A considerable fund of views and ideas about plesiomorphic and apomorphic traits and of trends within the Chironomidae, and the lower Diptera generally, was already to be found in the literature. Thus, I did not have to start from scratch. On the basis of what I considered to be synapomorphies and consistently searching for the sister group and its area of distribution, I worked out the hierarchies uniting the species within the Podonominae, Aphroteniinae, and Diamesinae. The result was, of course, hypothetical. But the situation changed drastically as the three hierarchies, thus erected, were compared and their geographical distributions were considered. It turned out that the three groups on the one hand and all their vicariant subgroups on the other, showed the same pattern of geographic vicariance and of phylogenetic relationship. In other words, an ordered similarity emerged that demonstrated a definable shared history, implying, for instance, that groups, now divided by vast expanses of ocean, once became separated from each other in an ordered sequence. These results, which could hardly be ascribed to chance, showed that the phylogenetic reconstruction ought to be correct in the main. I felt this a great success.

The following patterns were demonstrated by the phylogenetic analyses. (1) Each of the subfamilies contain representatives of a group in South Africa which is the sister group of a monophyletic group that includes representatives of the corresponding subfamily in South America, Australia/Tasmania and New Zealand. This pattern shows that the South African groups were severed from all connection with their southern relatives at a very early stage. (2) All the New Zealand groups have their closest relatives, their sister groups, in South America, and are in several cases clearly plesiomorphic; some of the groups show unique features, indicating long isolation. (3) The Australian groups also have their closest relatives in South

America, but they are all of them sister groups of a subordinate part of an older group in South America, and are all comparatively apomorphic. This indicates that the connection (by way of east Antarctica) between the Chironomid fauna in Australia and that of South America was broken at a comparatively late stage, and that the Australian groups are all derived from South American groups.

When I began my investigations around Antarctica, it was an open matter to me, as a non-geologist, whether Wegener's theory about continental displacements was acceptable or not. When my results were summed up, however, so much new evidence had been presented supporting this theory, and the former existence of a large southern continental block, Gondwanaland, that I found no reason to hesitate. The breakup sequence of the southern continents found by geophysicists and geologists fitted the evolutionary sequence of vicariance patterns in southern Chironomid groups, demonstrated on purely biological evidence.

That Antarctica played a significant role in the early evolutionary history of the biota of Gondwanaland is unquestionable. But my assumption that the family Chironomidae had been part of this process might be considered risky since this presupposes that the Chironomids are a very ancient group, existing during the Jurassic period, 140–180 million years ago. After all, ancestors of the groups studied by me must have been around when South Africa was separated from east Antarctica in the uppermost Jurassic, and one must presume that the Chironomids were quite advanced and diversified when New Zealand separated from west Antarctica in the upper Cretaceous, about 80 million years ago. Direct evidence of the great age of Chironomids was given, however, with the find of a revealing fossil (see below).

So, *mutatis mutandis*, we have reason to believe that additional groups of animals and plants, showing a southern vicariance pattern homologous to that of the Chironomids, are considerably older than supposed, and have a similar history.

It may be added that the trans-Antarctic relationships of these Chironomid groups clearly indicate that east and west Antarctica have served as two separate biogeographic provinces, implying that South America, through Patagonia, was in contact with Australia by way of east Antarctica, and New Zealand was in contact with Andean South America across west Antarctica. This is confirmed by the fact that east and west Antarctica constitute two separate geological provinces. Geologists now believe that west Antarctica has drifted independently of east Antarctica.

The results of the "Gondwana project" was presented in 1966 in a major treatise titled "Transantarctic relationships and their significance, as evidence by Chironomid midges. With a monograph of the subfamilies Podonominae, Aphroteniinae, and the austral Heptagylae" (Brundin, 1966).

With the publication of this treatise I had joined the international fray. Praise was mingled with criticism from the biogeographers of the old school, for which Hennig was either an unknown entity or a disruptive revolutionary. The sharpest criticism came, not unexpectedly, from the well-known biogeographer Philip Darlington, whose "Biogeography of the southern end of the world" (Darlington, 1965) has been severely criticized by me. According to Darlington, I had, for instance, fatally overestimated the age of Chironomids and underestimated the importance of wind dispersal for the emergence of the vicariance patterns that I had investigated. In my answer, however (Brundin, 1972b), I could refer to the fact that a comparatively advanced Chironomid, belonging to the subfamily Podonominae



and closely related to a living species, had recently been discovered in amber from the lowermost Cretaceous (i.e. close to the Jurassic border) of the mountains of Lebanon. This, *c.* 130-million-year-old fossil proves that the evolution of the Chironomids was far advanced when Gondwanaland started to split in upper Jurassic–lower Cretaceous. And chance dispersal across oceans seems like unnecessary speculation in this context. It is enough to address the conformity of the distribution patterns and the fact that the groups found in New Zealand and Australia all have their closest relatives on the other side of the globe, in South America. The Tasman Sea on the other hand, separating Australia from New Zealand, is no more than 1600 km wide.

Hennig too, came under fire when his book on the principles and methods of phylogenetic systematics was published in an English edition, making it generally accessible and readable (Hennig, 1966). That criticism was often based on unwarranted misunderstandings by those who for no good reason considered themselves as experts; else it concerned Hennig's logical conclusion, that only a strictly phylogenetic classification could serve as a general biological reference system.

Since 1966, I have had the opportunity, at conferences and as an invited speaker in many countries, not the least in the U.S.A. and Canada, to explain and defend Hennig's edifice and to be emphatic about the need for employing his principles and methods, especially in biogeography, which my own research has demonstrated. I also treated the subject in a series of papers (Brundin, 1968, 1970, 1972a,b, 1974, 1975a,b, 1981). It is gratifying to find that the understanding of these matters has increased rapidly in recent years. This is especially true for the USA, where the American Museum of Natural History in New York has become an active centre for further development.

Finally, I conclude that the importance of the Chironomids as biogeographic indicators fully equates to that of being ecological indicators. Midges are a remarkable group of insects and their investigation creates broad vistas into the conditions and history of life in time and space. Among the evolutionary aspects that have emerged, I finally wish to expand on the following theme (Brundin, 1974), vitalized through my study of Chironomids.

Since its origin on Earth, life has appeared in a dizzying number of different forms due to a continuous evolutionary process. Important in this connection is the fact that the immense "horizontal" hierarchy of plant and animal species that now surround us mirrors, even if incompletely, the "vertical" hierarchy that has evolved during aeons. We are surrounded by an imposing series of different types of organization, from utterly primitive organisms lacking a differentiated nucleus up to the most advanced Vertebrates. The large-scale persistence of primitive organisms is of great importance, not least by creating basal food supplies for numerous consumers. But the conservative trend also plays a crucial role in the speciation process, when life incessantly experiments with attempts at change and adaptation to new environments. As isolated populations are hit by mutations, the result is often fatal, but the point is that the mother population survives, and so new experiments are possible. But the result of a lucky outcome is a pair of species where one species is comparatively primitive, while the other is comparatively derived. In phylogenetic analysis we constantly encounter instances of this divergence between the two alternatives that are open to evolution.

The universal activity of this dual trend towards conservatism and change,

respectively, is stressed if we ponder its deep influence on human existence, now and before. Within different civilizations there have always existed a conflict between traditions and new ideas, between conservatism and the striving for change. Whenever this conflict has led to political and social unrest, however, humanity has always realized that it is impossible to break completely with traditions and the experience of former generations, that experiment and change often lead to disaster if they are too daring or too radical and that—all things considered—a balanced interplay between the two alternatives is of utmost importance for a harmonious coexistence. But both alternatives are vital; just like Chironomids, man is subject to the fundamental principles of life.

## REFERENCES

- BRUNDIN, L. Z. 1934. Die Coleopteren des Torneträskgebietes. Ein Beitrag zur Ökologie und Geschichte der Käferwelt in Schwedisch-Lapland. Carl Bloms Boktryckeri, Lund.
- BRUNDIN, L. Z. 1942. Zur Limnologie jämtländischer Seen. Meddelanden från Statens Undersöknings—och Försöksanstalt för Sötattensfisket 20: 1–104.
- BRUNDIN, L. Z. 1947. Zur Kenntniss der schwedischen Chironomiden. Ark. Zool. 41A: 1–95.
- BRUNDIN, L. Z. 1948. Über die Metamorphose der Sectio Tanytarsariae connectens (Diptera, Chironomidae). Ark. Zool. 39A: 1–22.
- BRUNDIN, L. Z. 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. Ein Beitrag zur Kenntniss der bodenfaunistischen Charakterzüge schwedischer oligotropher Seen. Rep. Inst. Freshwat. Res. Drottningholm 30: 1–914.
- BRUNDIN, L. Z. 1956a. Die Bodenfaunistischen Seetypen und ihre Anwendbarkeit auf die Südhalkugel. Rep. Inst. Freshwat. Res. Drottningholm 37: 186–387.
- BRUNDIN, L. Z. 1956b. Zur Systematik der Orthoclaadiinae (Dipt. Chironomidae). Rep. Inst. Freshwat. Res. Drottningholm 37: 5–185.
- BRUNDIN, L. Z. 1958. The bottom faunistic lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity of lakes and oceans. Verh. Int. Ver. Limnol. 13: 288–297.
- BRUNDIN, L. Z. 1966. Transantarctic relationships and their significance, as evidenced by Chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagviae. Kongl. Svenska Vetenskapsakad. Handl. (4) 11: 1–472.
- BRUNDIN, L. Z. 1968. Application of phylogenetic principles in systematics and evolutionary theory. In: T. Örvig (ed.). Current Problems of Lower Vertebrate Phylogeny. Almquist and Wiksell, Stockholm, pp. 473–495.
- BRUNDIN, L. Z. 1970. Antarctic land faunas and their history. In: M. W. Holdgate (ed.). Antarctic Ecology. Academic Press, New York, pp. 41–53.
- BRUNDIN, L. Z. 1972a. Evolution, causal biology and classification. Zool Scr. 1: 107–120.
- BRUNDIN, L. Z. 1972b. Phylogenetics and biogeography. Syst. Zool. 21: 69–79.
- BRUNDIN, L. Z. 1974. Fifty year's limnic zoogeography. Mitt. Int. Verein. theor. angew. Limnol. 20: 287–300.
- BRUNDIN, L. Z. 1975a. Phylogenetische Biogeographie als Glied der Evolutionsbiologie. Verh. Dtsch. Zool. Ges. 67: 372–380.
- BRUNDIN, L. Z. 1975b. Circum-Antarctic distribution patterns and continental drift. Mém. Mus. Nat. Hist. Nat., Sér. A, Zool. 88: 19–28.
- BRUNDIN, L. Z. 1981. Croizat's panbiogeography versus phylogenetic biogeography. In: G. Nelson and D. E. Rosen (eds). Vicariance Biogeography—A Critique. Columbia Univ. Press, New York, pp. 94–138.
- DARLINGTON, P. 1965. Biogeography of the Southern End of the World. Distribution and History of Far-southern Life and Land, with an Assessment of Continental Drift. Harvard Univ. Press, Cambridge, Massachusetts.

- HENNIG, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.
- HENNIG, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. Beitr. Entomol. 3, Sonderhaft: 1-85.
- HENNIG, W. 1957. Systematik und Phylogenese. Ber. Hundertjahrf. Dtsch. Entomol. Ges. (Berlin, 1956): 50-71.
- HENNIG, W. 1966. Phylogenetic Systematics. Univ. of Illinois Press, Urbana.