Jacob Christian Schäffer was the first to appreciate the morphological complexity of the microscopic crustacean *Daphnia*. His investigations, published in 1755, provide an excellent example of the difficulties facing those who, for the first time, attempted to elucidate the structure of extremely complicated animals of small size, of which there were no familiar counterparts. Nevertheless he not only revealed many hitherto unsuspected anatomical features but attempted, with some success, to explain their function. Most notably he showed that *Daphnia* produces a current of water that draws suspended particles into its complex food-handling machinery. An earlier suggestion of how it feeds was completely erroneous and misleading. A pioneer of the comparative method, Schäffer provided an excellent example of how it helped him to understand, if not entirely to resolve, a complicated mechanism. That reproduction can be either parthenogenetic or sexual presented problems that were not resolved for more than another century. Unaware that males exist, and on the basis of seemingly sound, but misleading, observations, he concluded that *Daphnia* is a hermaphrodite.

**Keywords:** J. C. Schäffer; micro-anatomy of *Daphnia*; observations on function; reproduction

**INTRODUCTION**

Although Jacob Christian Schäffer (1718–90) is held in high esteem by mycologists, by whom he is remembered particularly as the author of a four-volume work on the larger fungi and as the describer of numerous previously unknown species, and has not been entirely forgotten by entomologists, he otherwise receives scant attention in accounts of the history of biology. However, his contributions were numerous, diverse, and often greatly in advance of anything previously recorded in the fields covered by his investigations. Nowhere is this better seen than in his studies of freshwater crustaceans, which reveal him as an acute observer, a competent microscopist, an anatomist with a lively appreciation of function, and a naturalist with a keen interest in how animals conduct their lives. These studies, which not only revealed previously unsuspected morphological complexity but also made significant progress towards elucidating its significance, had no predecessors, nor were they emulated to
any significant extent until well over half a century later, and not surpassed for considerably
longer. The extent of these discoveries and their pioneering nature seem never to have been
realized, yet Schäffer was undoubtedly one of the most successful of eighteenth-century
micro-anatomists and had a real understanding of the significance of the structures and
mechanisms that he revealed, and of the lifestyles of the animals concerned. He greatly
advanced our knowledge of microscopic crustaceans, many of his discoveries revealing, and
sometimes resolving, complexities that were previously entirely unknown.

**SCHÄFFER’S CAREER IN A NUTSHELL**

Although Schäffer (figure 1)—born on 30 May 1718 in Querfurt, near Halle in Thuringia—
produced a large volume of scientific work that embraced several disciplines, he received no
formal education in either science or medicine. He studied at the French School of Latin in
Halle, Germany, and as a student of theology at the University of Halle. In 1738 he became a
private tutor in Regensburg (=Ratisbon) in which town he resided thereafter, becoming
pastor of an evangelical church in 1741, and superintendent in 1779. In 1760 and 1762 he was
awarded doctorates in philosophy and theology by the universities of Wittenberg and
Tübingen, respectively. Although he had no formal scientific training he eventually had
contacts with medicine through his immediate family, of whom three became distinguished
physicians. His younger brother, Johan Gottlieb, began to train as a pharmacist in 1734 at the
age of 14 years, presumably as an apprentice, took over a pharmacy in Regensburg in 1741
and, with Jacob Christian’s support, subsequently studied medicine in nearby Altdorf. He
established a practice in Regensburg in 1745, where, in 1763, he introduced what has been
recorded as smallpox vaccination but which was presumably variolation because Jenner did
not announce his work on vaccination until 1798. He published various works on medicine,
including, in 1752, a book on the effects of electricity on the human body and its ailments.
Johan Gottlieb had two sons who also became physicians of some eminence, both of whom
practised in Regensburg, as well as holding other appointments of distinction, and both
published books on aspects of medicine.

Schäffer’s proposer for Fellowship of the Royal Society, to which he was elected in 1764, was
Charles Bonnet, a Swiss biologist often cited as the discoverer of parthenogenesis during his
work on aphids, who did indeed elucidate details of this phenomenon but had been anticipated in
various ways by the versatile Antoni van Leeuwenhoek FRS. His proposer was thus a foreigner
and the proposal was written in French. Schäffer was associated with other scientific academies
and societies in Germany and elsewhere in Europe, which, as was then the custom, were
sometimes listed on the title page of his works. The impressive number of his affiliations
indicates that his scientific abilities were widely recognized by his contemporaries.

**THE SCOPE OF SCHÄFFER’S SCIENTIFIC INVESTIGATIONS**

In spite of the demands on his time called for by his vocation, Schäffer’s scientific output was
prodigious. Brief mention of some of his multifarious investigations and achievements
reveals the extent and importance of this work, much of which was of a pioneering nature.
Although his biological studies embraced a great diversity of organisms, he was no dilettante.
As well as his work on fungi and higher plants and the production of a book on herbs and
pharmacy, he made a remarkably detailed microscopical study of the tube-building rotifer
*Floscularia ringens*, investigated *Hydra*, the liver fluke of sheep, molluscs, a wide range of
insects including beetles, bees and ascalaphids, made studies on the life history of a moth and
the Apollo butterfly, and wrote a three-volume work on the insects of the Regensburg area,
another on the elements of entomology, and others on fishes and birds. Aided by attractive
colour plates by competent artists, his book on ornithology described avian anatomy and
included a section on the local avifauna that covered such topics as nidification and migration.

Although this incomplete survey of his biological publications indicates his productivity,
it does less than justice to his versatility. He wrote on the theory of colours, experimented
with electricity, was interested in such practical things as lens grinding, invented a washing
machine and a mechanical saw, and suggested improvements in domestic ovens. Particularly

Figure 1. Jacob Christian Schäffer.
noteworthy is his attempt to find substitutes for the rags that were then used in papermaking, of which it was becoming increasingly difficult to obtain sufficient quantities. He experimented with the use of hairs of the black poplar and the down of cottongrass and, more significantly, inspired by the making of paper from wood by wasps that had been observed by Réaumur in 1719, attempted to use the wood of beech and willow for this purpose. Between 1765 and 1771 he wrote six small volumes that included samples of paper made from different fibres. His efforts were derided by traditional papermakers, who continued to use rags, and it seems that to some of what he believed to be rag-free or low-rag papers, rags may have been surreptitiously added by his helpers, either to facilitate their work or so that he would be pleased with the results! Nevertheless, Renker considers him to be the inventor of wood paper, which became a practical reality some 80 years after his experiments. All this was in addition to his producing theological works and funeral orations as part of his vocation. Clearly interested in bringing scientific matters to the attention of his parishioners and others, he also established a museum that was open to the public.

SCHÄFFER’S STUDIES ON WATERFLEAS AND RELATED CRUSTACEANS

It is perhaps his curiosity-led studies on what are popularly known as waterfleas that best reveal Schäffer’s biological competence and diverse talents. They also resulted in enlightening discoveries. Moreover, as his predecessors were few, and their contributions slight, he was the first to gain a truly scientific appreciation of these tiny animals. The term waterflea, which has no scientific validity, is generally used as a popular name for Daphnia and its immediate allies, and Schäffer used the name Wasserflöhe in this sense. To consider his work against the little that was previously known not only reveals his achievements but provides an enlightening picture of how the early microscopists began to grope for an understanding of, first, the anatomy of a group of extremely complex animals, and, somewhat later, of how they functioned. It also reveals the difficulties and pitfalls that beset these investigators, who included a surprising number of Fellows of the Royal Society. A brief history of early observations on Daphnia puts Schäffer’s work in context and shows how slowly knowledge was acquired.

Species of Daphnia, of which some 20 of the 75 or so described species are native to Europe, are branchiopod crustaceans that belong to the order Anomopoda. They frequent a wide range of standing waters, from large lakes to small ponds, occupy a diversity of niches, and sometimes occur in prodigious numbers. Adult females of most species are 2–3 mm in length, but those of D. magna occasionally exceed 5 mm. Males are smaller.

It has been claimed that Goedart was the first to mention, and even that he illustrated, Daphnia in 1662, but the first claim is dubious and the second incorrect. A previously unchampioned claimant could be Henry Power FRS, who, in his Experimental Philosophy (1664) refers to the occurrence in ponds in summer of ‘an innumerable company of little whitish Animals which move up and down the water with jerks and stops in their motion; in which Animals we could discover two little horns and legs, but never could get to see it quick in the Microscope, for as soon as it is taken out of the water it is perfectly dead.’ The description fits Daphnia, but cyclopoid copepods, which seem less likely contenders, cannot be ruled out.

The earliest illustrations of Daphnia (figure 2) were provided in 1669 by Jan Swammerdam, who is famous for his superb dissections and illustrations of a wide range of animals, including humans. Considering that they had no predecessors, these have considerable merit. Not surprisingly, however, they also have defects, some of which
illustrate one of the pitfalls into which these pioneers not infrequently fell. They had no previous conception of anything like *Daphnia*, and in seeking to interpret what they saw they sometimes did so by making comparisons with familiar organisms. To Swammerdam the pointed rostrum of the head was reminiscent of the beak of a bird. Imagination did the rest and he drew it like a sharp beak. He thought that this was a hollow structure through which *Daphnia* sucked its food, as do certain insects. Although this suggestion was completely erroneous, he correctly described how it swims by means of its antennae, and recognized that the trunk and its limbs lay free within the chamber enclosed by the carapace. However, he thought it had two eyes—albeit joined to each other—though it has only one. That such an outstanding naturalist as Swammerdam could misinterpret *Daphnia* in such ways is an excellent reminder of how difficult it was for early investigators, provided as they were with still crude microscopes, to interpret these then utterly strange and complex animals correctly. (How his illustrations were posthumously modified is noted in the legend to figure 2.)

In 1684 Francesco Redi\(^6\) gave three crude but recognizable illustrations of *Daphnia* that, although avoiding imaginative interpretations, were less informative than those of Swammerdam. In 1699 Antoni van Leeuwenhoek\(^7\) removed embryos from the brood pouch of what was probably a *Daphnia*, whose beating heart he observed, but otherwise said nothing about its anatomy. In 1721 Richard Bradley\(^8\) FRS described and ‘delineated with all possible Exactness’ a *Daphnia* of which he in fact produced a grotesque illustration (figure 3), accompanied by equally fanciful comments. He described the head as being ‘somewhat like
that of a Bird’ and ‘the parts which seem to do the Office of Legs and fling the Creature forward ... by regular Springs or Jirks’, which they do not, as ‘almost like the claws of an Eagle, and are two in Number, placed on each side of the Belly’. The supposedly Eagle-like ‘claws’, drawn as such, bear scant similarity to the median post-abdomen. The true legs remained undetected. The arborescent antennae, by means of which it in fact propels itself, as Swammerdam made plain, whose action Bradley failed to notice, were said to resemble ‘the Dugs of Animals’ and he supposed them to be ‘designed for suckling their young’—a fanciful suggestion doubtless inspired by the fact that he at least knew the animal to be viviparous. That some individuals may have been males seems not to have been considered.

The remarkable memoir on Hydra produced by Abraham Trembley9 FRS in 1744 included a minuscule illustration of Daphnia, which he used as food for his polyps. Although he said little about its structure, he provided, almost as an aside, interesting comments on its habits, and reported the results of some simple experiments, the first ever conducted on Daphnia, which revealed certain reactions to light. Until recently pointed out, these had gone unremarked, for the obvious reason that readers of his memoir are interested mostly in Hydra and not in Daphnia. Lenhoff and Lenhoff11 regard Trembley’s work on Hydra as marking the beginning of experimental zoology: in that beginning Daphnia can claim a humble place.

In 1753 Henry Baker12 FRS gave an illustration of Daphnia, whose level of accuracy can be judged by the fact that he believed it had two eyes. Even Bradley knew it had only one, which is derived from two eyes that fuse in the embryo. Apart from a posthumous work by Joblot13 in 1754, which included a crude illustration, Schäffer had no other predecessors. His account, published in 1755,14 is truly remarkable. Reflecting his eclectic interests, it is part of a memoir that dealt not only with Daphnia and another daphniid that now resides in the genus Simocephalus but also with Hydra and the oligochaete worm Tubifex, which he referred to as a Wasseraal.

Although we know little about how Schäffer conducted his investigations, or what instruments he used, a few reasonable deductions can be made that put these matters within the context of the times. He clearly employed a compound microscope, probably of the

Figure 3. Richard Bradley’s illustration of Daphnia of 1721. Lower figure approximately life size.
Culpeper type, introduced in about 1725 and widely used for about a century. The body, originally of turned wood, and only in later models of brass, carried the eyepiece, field lens, and an interchangeable objective lens of which different versions gave different magnifications. For focusing, this simply slid up and down inside a pasteboard tube (made of layers of old paper) covered with leather or fish skin. This assemblage stood on three legs above the stage, which, well elevated on a tripod usually made of brass, had a hole in the middle above a light-collecting adjustable mirror, itself a recent innovation. Such a microscope, with a telescope, globe and armillary sphere, is illustrated for example in the title page engraving of the first publication of the Königlich Societaet der Wissenschaften of Göttingen in 1751, which was officially launched in 1752 at about the time that Schäffer was engaged on his studies, and indicates the kind of instruments available in Europe at that time. If he was very up to date he might have possessed a Cuff microscope—introduced about 1743—or a continental copy. These had a brass body, carried on a side pillar, employed rack and pinion and fine thread screw focusing, and had a stage that was not ‘fenced in’ by the three supports of the Culpeper type. These advantages were not, however, accompanied by advances in lens quality. Achromatic combinations of lenses were not to appear in telescopes until 1758; because the smaller lenses of microscopes presented a more difficult challenge to lens makers, they did not feature in these instruments until about 25 years later and were not commercially available until the early nineteenth century. The images observed by Schäffer certainly suffered from chromatic aberration as well as from spherical aberration—a defect not overcome until much later. A simple lens was probably used for observing Daphnia and other animals under water in glass vessels. Such a lens on a stand would be an aid to dissection. How he killed animals before dissection is not stated; hot water may have been used. He says nothing about his dissecting implements, which would inevitably have been simple—probably fine needles mounted on suitable handles. He tells us that he dissected out mandibles—no mean feat—for which and for other delicate operations steady hands and patience were probably his greatest assets, but could only be exploited after achieving intimate familiarity with the anatomy of the animals as a result of persistent observation.

Like the pioneer microscopist van Leeuwenhoek he employed an artist, in this case J. G. Bez, whose drawings were engraved on copper and later coloured. Illustration must have been a complicated business because Schäffer would have had to make an observation and explain it, or do a dissection, and then instruct his artist to draw it, using the microscope. These difficulties notwithstanding, his illustrations are much superior to, and vastly more informative than, any of their predecessors.

The animal studied is readily recognizable as D. magna, of which Schäffer was the original describer. However, as this was before the introduction of binomial nomenclature to zoology in 1758, he referred to it as die geschwänzten zackigen Wasserflöhe (the tailed, branched waterflea). The adjective ‘branched’ refers to the locomotory antennae. The name D. magna was bestowed in 1820 by Strauss, who therefore stands as its author.

Schäffer’s Plate I, reproduced here as figure 4, shows D. magna at about actual size (Fig. I) and, more highly magnified, as it swims (Fig. VI and Fig. VII), which it does for the most part with its longitudinal axis aligned more or less vertically, or with the head inclined somewhat forward. These illustrations, much superior to their forerunners, give a good three-dimensional impression of the animal in life, and even today are seldom emulated because Daphnia is generally portrayed in lateral view—which has various advantages but is less lifelike, and is easier to produce. In assessing the significance of these illustrations it must be remembered that, apart from crude figures of the whole animal, most of which were not
merely unhelpful but positively misleading, he had nothing to guide him. The drawings of anatomical details had no predecessors. Moreover, throughout his work he showed splendid independence of mind and refused to accept uncritically the opinions of others. This truly scientific attitude is made clear by reference to a simple feature of the head. He criticized the

Figure 4. Schäffer’s Plate I. This shows (Fig. I, a–g) a group of Daphnia magna, about life size, swimming in various directions; (Fig. VI and Fig. VII) females more highly magnified, drawn from life, showing oblique ventral and oblique dorsal views respectively; (Fig. VIII) a female with its right carapace valve removed to reveal the trunk limbs and post-abdomen within the carapace chamber, and showing the minute protozoans and rotifers that sometimes frequent the carapace; (Fig. V) two females that have become entangled, which caused Schäffer to believe that mating was taking place and that Daphnia is a hermaphrodite; (Fig. I, h) an ephippial female; (Fig. II, Fig. III and Fig. IV) eggs and early development; and (Fig. IX) Simocephalus vetulus.
illustrations of Swammerdam, Baker and, as he put it with evident respect, even of Trembley, then still alive (‘und selbst die Abbildungen von Herr Trembley’), all of which portray the rostrum as sharply pointed. He made it clear that he was not able to persuade himself that these authors were correct or that each had not copied from his predecessor without examination of the animal. This was a little hard on Trembley, whose illustration, again by an artist, was minute so as to indicate actual size, and was certainly not of *D. magna*. However, Schäffer correctly maintained that he did not know how to reconcile these illustrations with what he had seen with his own eyes. In this he was somewhat inconsistent in apparently assuming that all investigators were dealing with the same species—which might have been justified at that time had he not himself illustrated the head of a second species in his Plate II, Fig. I.

Schäffer revealed many anatomical details of previously unknown structures. His Fig. VIII in Plate I (figure 4 in this account) is of a mature female, the right valve of whose carapace has been removed to reveal what lies within. It shows the location of the trunk limbs, which are extremely difficult to portray *in situ*, and the post-abdomen. This figure is the first to illustrate the minute antennules (a). It also shows some of the protozoans (h) and rotifers (k) that sometimes frequent the carapace. The latter, clearly recognizable as *Brachionus*, are shown, more highly magnified, in his Plate II (here figure 5), Fig. VII, Fig. VIII and Fig. IX. In Europe the *Daphnia*-frequenting species is invariably *B. rubens*. These are the first illustrations of what are now called epibionts. Also illustrated on the first plate are eggs (Fig. II) and embryos (Fig. III) removed from the brood pouch of parthenogenetic females, and a juvenile (Fig. IV) showing, correctly, the relatively longer carapace spine of early instars. Growth of this spine is allometric.

Drawings that illustrate Schäffer’s advances in understanding far beyond anything previously known appear in his Plate II. For the first time he not only revealed how complex these animals really are but also began to elucidate the significance of that complexity. His Fig. II shows details of the head and adjacent structures of *D. magna*, whose cuticular headshield he likened to the veil of a nun. Many structures are identified, including the alimentary canal, its caeca, the compound eye and the muscles that keep it in constant motion, the ocellus or eyespot, the right mandible, the heart and the cerebral ganglion. Also shown is the position where the antenna arises—labelled (k) in Fig. I—which portrays the head region of another species. A detached antenna is shown as Fig. VI. Not only had most of these structures never previously been illustrated, most investigators had been completely unaware of their existence. Indeed, the ocellus was overlooked 65 years later even by the careful Jurine, who noticed its more conspicuous homologue in what are now recognized as related genera.

Schäffer was not only the first to reveal what lay within the carapace chamber and to provide a remarkable account of what he found, but he made a praiseworthy attempt to interpret its significance and to provide some inkling of how *Daphnia* actually collects its food. Figure II of his Plate II (figure 5) indicates the region (v), just posterior to the head, where he observed that a stream of water, and the particles that it carried, flows into the cavity bounded by the carapace valves. No earlier observer had even suspected this. What is particularly striking is that, in itself, this need not necessarily have told him anything about the feeding mechanism. Hitherto no one had had any idea of what *Daphnia* ate, let alone how it handled its food, and it will be recalled that Swammerdam had formed a completely erroneous idea of its feeding habits. Schäffer must have noticed that the gut was full of finely particulate material, often black in *D. magna* (sometimes green when algae are plentiful, but more often so in open water species). He had also seen the ejection of faeces—a frequent event—and noticed their similarity to the gut contents. This must have alerted him to the fact...
that the current-borne particles that he saw entering the carapace chamber could be the animal’s source of food. This he confirmed when he observed accumulations of such particulate material passing forward deep within the chamber. Although he does not here
illustrate the trunk limbs, which, five pairs on each side, lie almost immediately posterior to
the head, as shown in Fig. VIII of his Plate I (figure 4), he indicates an accumulation of food
(u) coming from what he refers to as the second or third pairs of trunk limbs (which he calls
Kieffenfüsse, jaw feet). This passes forward along a ventral groove of the thorax—the food
groove—towards the mandibles (which he calls Zähne, teeth). After passing between the
mandibles he notes that its movement changes direction and it begins to move upwards.
These are entirely new observations of a high order.

Figure IV of his Plate II (figure 5) is the first illustration of isolated trunk limbs, of whose
very existence others had scarcely been aware. What is more, Schäffer attempted, with
considerable success, to ascertain how they were arranged with respect to each other.
Although, not surprisingly, he seriously misinterpreted certain features, the attempt revealed
that Daphnia possessed structures of hitherto unimagined complexity. The righthand series
of appendages is shown as seen in face view from the midline. Of the five pairs, the structure of
the posterior three is remarkably well elucidated and is very revealing. Limbs 3 and 4 bear
large filter plates and these are extremely well portrayed. It is these filters that, by a
complicated process, extract suspended particles brought into a cage-like filter chamber by
the current that he was the first to detect. Not only the arrangement of the setae but their
armature of setules, which make up a very fine-meshed filter, are clearly shown, although
Schäffer did not appreciate how they operated. In this he was not alone. Almost a century later
William Baird16 (later FRS), who had Schäffer’s work and that of Jurine15 to help him, and
whose artist was able to illustrate each separated limb, still had no idea that these elegant
structures were filters and, like De Geer17 before him, believed that they served as gills.

Although the gnathobasic (basal) region of trunk limb 2 was in part well shown, Schäffer
failed to discriminate between limbs 1 and 2, which he conflated into a single structure. What
he portrayed and labelled as the first limb is something of a mystery. It is not the maxillule, a
minute appendage that lies in approximately that position but has only three spines, whose
presence escaped detection. A possible explanation is that part of the second limb of the left
series, perhaps folded and distorted, found its way into the preparation. Apart from this his
dissection and its interpretation was a major step forward.

Having recorded how food material derived from the suspended particles is drawn between
the trunk limbs, accumulates and passes forward—as illustrated (u) in Fig. II of his Plate II
(figure 5)—Schäffer noted how it reaches the mandibles. These he illustrated, correctly
orientated, in Fig. III with their masticatory surfaces opposed to each other. The delicate task of
isolating these minute chitinous structures was facilitated by using an individual that had died
and had lain for several days in the water, whose muscles must largely have disintegrated. He
informs us that he removed them with little trouble. His illustration clearly shows their hollow,
boat-like nature. He described the pointed pivot (a) as the root (Wurzel), and the masticatory
region (d) as the crown (Krone). He recognized that the latter had a flattened region (vorderere
Platte) that was not smooth but had an irregular surface like, as he put it, the molar teeth
(Backenzähne) of ‘other animals’—implying mammals. The molar surface of the right mandible
(Mand) can be seen in figure 6 (made well over 200 years later) at the anterior end of the food
groove (FG) and near the entrance to the oesophagus (Oe). He recorded that the mandibles are
semi-transparent save for the crown, which is brown and opaque. Here the chitin is sclerotized
for toughness. No previous investigator had any idea that Daphnia even possessed such structures.

Schäffer, however, did more than simply report the existence of the mandibles. He clearly
understood the basic principles of their mode of action, which can be seen in the living
animal. He described how they rotate on their pivots and how their masticatory surfaces
Figure 6. The general morphology of *Daphnia longispina*, as revealed in a bisected individual; showing the right-hand half of the animal from the midline and the arrangement of the trunk limbs, of which limbs 3 and 4 (TL3 and TL4) bear conspicuous filters. These, and their counterparts on the left side of the body, make up a median chamber or cage into which water is drawn. As it leaves the chamber via the filter plates (FP3 and FP4), suspended particles are retained as food. Each of the long filtering setae that make up these filter plates bears on each side a row of minute setules (omitted from the illustration) so that each plate is a fine meshed filter. (Reproduced from Fryer\textsuperscript{18}; copyright © The Royal Society.)
continually thrust or rub against each other, and he went on to describe how, as a result of these movements, food brought to them by the trunk limbs passes between their opposed masticatory regions, and how, emerging after doing so, it enters the oesophagus, for whose entrance he used the term Schlund (throat or gullet). He then went on to describe the route subsequently taken by the food by referring to an illustration, noting its passage from the oesophagus to the much wider and longer mid-gut, which he designated as the stomach (Magen), and, having passed through this to what he called the rectum (Mastdarm), material is voided as faecal matter from the anus (k) located near the end of the post-abdomen (Fig. V). When this well-illustrated structure, which Schäffer called the Klauenfuss, is compared with the almost medieval grotesqueness of Bradley’s paired Eagle-like talons described less than 30 years earlier, one realizes the magnitude of the advance in understanding that he had achieved. He rounded off this aspect of the story by contrasting his accurate recital of events with Swammerdam’s very different suggestion that food is sucked through a tubular structure.

Although, not surprisingly, he did not fully elucidate the feeding mechanism, the merit of Schäffer’s achievement can be understood by bearing in mind that his investigations into the nature of these limbs had no previous work to guide it. One must also remember the minute size of the appendages involved and the limitations of the optical equipment then available. Late twentieth-century studies that have shown how these complex structures are actually arranged18 (figure 6) emphasize the difficulty of his task. Indeed, in 1778 De Geer17 conceded that, in spite of all his patience, it was not possible for him to distinguish the parts of the limbs as well as had Schäffer, whose illustrations he praised. He also confessed that he was unable to disentangle the form of the mandibles or to elucidate their movements. Nothing puts the matter better into context than Jurine’s15 comment 65 years later, after his own investigation of the problem—’L’organisation des pattes est si compliquée, qu’on doit presque désespérer de la bien faire comprendre’. Nor did he succeed in doing so. For example, he believed that legs 3 and 4 had the same structure.

In seeking to explain how he believed Daphnia deals with its food, Schäffer drew on his knowledge of other branchiopods on which he had already made equally pioneering observations, thereby providing an early example of the comparative approach that has since proved so fruitful in functional studies. He had already published an account in Latin of a fairy shrimp (a member of the Anostraca),19 which, in a German version of 1756,20 he was to call the fischformige Kiefenfuss, now appropriately known as Branchipus schaefferi. This is an animal much larger than Daphnia, and of even more ancient antecedents, that has a series of 11 pairs of similarly constructed, fully exposed, trunk limbs. He had also studied two notostracans, Triops and Lepidurus, sometimes called tadpole shrimps, on which a substantial publication was to appear in 1756.21 These, also much larger than Daphnia, have a carapace that covers the anterior part of the trunk, and numerous trunk limbs. Unlike Branchipus, which swims inverted and therefore readily displays its limbs, Triops, which he called the krebsartiger Kiefenfuss mit der kurzen Schwanzklappe, generally swims with its trunk limbs close to the bottom, but obligingly reveals their movements if held dorsal side downward. Although the details are very complicated, Schäffer was already familiar with the way in which the food taken between the trunk limbs of both these groups is passed forward from limb to limb and eventually to the mandibles. Although the details are very different in Daphnia, a similar route is followed. Passing food along a ventral food groove is indeed a deep-seated attribute of the Branchiopoda, a very ancient group of crustaceans, and this device Schäffer was the first to see and, in essence, to comprehend. In an enlightening passage he reports how, during certain summers, when
representatives of both the Anostraca and Notostraca were available, he had had the rare opportunity to study them and had already described the feeding process in his fairy shrimp, fairly comprehensively (ziemlich begreiflich) and intended to do so for his notostracans, which he did in 1756. When he saw their mandibles at work this led him to wonder whether his waterfleas (in which he percepiently recognized similarities to their larger relatives) might display similar attributes. With these thoughts in mind he subjected them to further inspection and discovered their mandibles.

Schäffer was clearly delighted to locate the mouth of Daphnia and asks whether it is not probable that an animal whose mouth lies so deep within the body can have other hidden secrets, and whether one should always expect to find an animal’s mouth at the front of the head. Of the previously unknown mandibles, he made it clear that they are none other than the tools through whose action and rubbing together, food, brought thither by the trunk limbs, is triturated, and thence carried to the mouth. He went on to ask whether anyone can object to the claim that in this little animal (Daphnia) food is, to use modern terminology, taken within the carapace chamber, is collected between the trunk limbs (by which he means the two series of limbs), and is then brought forwards to the mouth. Considering that the only previous suggestion as to how Daphnia obtained its food was completely erroneous, and gave no clues as what really takes place, his findings were a tremendous achievement.

Notwithstanding his remarkable discoveries, Schäffer’s complicated account of how Daphnia handles its food is difficult to follow, and as his description of the trunk limbs is in part incorrect, and their functions are incompletely understood, the result is inevitably inadequate but nevertheless highly commendable. What is truly remarkable is that he was aware that current-borne particulate matter following a posteriorly directed route is intercepted by the trunk limbs that then pass it forwards to the mandibles. That he failed to elucidate details of the mechanism fully is not surprising. Although, 65 years later, Jurine appreciated various aspects of the feeding mechanism, his understanding of the process fell short of Schäffer’s. Indeed, not until almost two centuries after the latter’s pioneering work did it receive meaningful attention, when it was the subject of vigorous debate between Herbert Graham Cannon22 FRS and Otto Storch,23,24 both of whom greatly advanced understanding of this process, though neither provided a complete explanation. Apart from those of Lilljeborg25 in 1900, which, although meticulously accurate, were not produced with function in mind, Cannon’s were the first truly accurate three-dimensional illustrations of each isolated limb of Daphnia that revealed their nature and complexity.26 However, both Cannon and Storch, like Schäffer before them, to a large extent worked in an evolutionary vacuum. Daphniids are specialized anomopods whose feeding mechanisms, which enable them to collect suspended particles, are derived from those of ancestors that collected sedimented or attached material. Not until the work of Eriksson27 in 1934 did information on the feeding mechanisms of such anomopods begin to appear, enabling these devices to be considered in an evolutionary context.

Schäffer was the first to describe an anomopod of a genus other than Daphnia. Although he used the word ‘Gattung’, this was not in its present-day German usage as ‘genus’ but only to imply a ‘kind’ or ‘sort’ of animal. The species described is easily recognized as Simocephalus vetulus. Because its most obvious difference from Daphnia is the lack of a posterior carapace spine, he called it the ungeschwänzten zackigen Wasserflöhe (the tail-less—or spineless—branched waterflea) (figure 4; his Plate I, Fig. IX). Significantly he noted that it differed from Daphnia not only in form but in the way it swims (‘wie sie sich bewegen’), and he stressed its way of life and mode of locomotion. Simocephalus swims inverted, an attribute whose significance was not otherwise recognized until attention was drawn to it by Scourfield28 in
1900. Schäffer likened this posture to that of the very different anostracan, *Branchipus*, than which, as he noted, it moves more suddenly and faster. He also made the very significant observation that it attaches itself to objects and can even do so to the wall of a glass vessel. It spends much time so attached and therefore expends less energy in swimming than *Daphnia*, and so can afford a thicker, more protective, carapace and headshield, but employs a similar feeding mechanism. Like those on *Daphnia*, Schäffer’s observations on *Simocephalus* were entirely new, and his remarks on their different lifestyles were the first to throw light on the adaptive radiation of the Daphniidae. Both genera are multispecific, and the fact that it is possible to recognize both species from his account bears testimony to the accuracy of his observations and the skill of his artist.

Like those who were to follow him, Schäffer had confused ideas about the reproduction of *Daphnia*. In nature in the temperate zone it is predominantly parthenogenetic during the warmer months, but males appear as conditions deteriorate later in the year and mate with females, which then produce drought-resistant resting eggs, two in number, that are enclosed in a packet made by modification of part of the carapace. This, known as an ephippium, is shed at the next moult. Its eggs can tolerate freezing and desiccation for long periods, and they hatch when satisfactory conditions return. No male had been reported by any of Schäffer’s predecessors, nor did he encounter one. Having reared four successive parthenogenetic generations without being aware of the existence of this phenomenon, his suggestion that *Daphnia* is a hermaphrodite was a reasonable, but erroneous, conclusion. He mistakenly thought that he had located the exit of the male reproductive system on the post-abdomen of the female (his Plate II, Fig. V (i)) at the base of the long sensory setae (h) of that structure. Having never found a male—populations consisting entirely of parthenogenetically reproducing females are common in summer—when he saw what appeared to be pairs of mating individuals, and illustrated one such (his Plate I, Fig. V), they naturally seemed to confirm his belief that *Daphnia* is a hermaphrodite. However, both are females that presumably became entangled during handling of his captive animals. Males were not recognized until 1785, by Müller, who had strange ideas about them.

In Plate I (here figure 4) Schäffer illustrated an ephippial female (Fig. I (h)), being the first to do so, although the significance of the ephippium, shown too small, which he describes as a large black spot above the posterior spine, was unknown to him. Apparently he saw very few such females. By 1820, Jurine, who had paid considerable attention to the reproduction of *Daphnia* and who was apparently still only the second person to have seen a male, had seen many ephippial females as well as cast ephippia. As now seems obvious, the latter clearly contained two resting eggs. He had also seen ephippia produced by the related family Chydoridae, containing a single egg. However, such were the difficulties of elucidating anomopod reproduction that he failed to recognize these structures for what they were. He referred to the ephippium as a saddle (*selle*) and thought that ephippial females were individuals afflicted by a disease. Moreover, he chided Schäffer for not describing an ephippium—although he had in fact described and illustrated an ephippial female.

The kind of evidence that caused confusion to these early investigators can hardly be better demonstrated than by an excellent illustration of a male *Daphnia* mating with a female carrying a brood of parthenogenetically produced young that was made for Jurine by his daughter in 1820. This act had nothing to do with the production of such offspring. The ephippial eggs that do result from such matings, also seen by Jurine, were not recognized by him as such. Even in 1850, by which time males were well known and the role of the ephippium had been elucidated, Baird, who studied the reproduction of *Daphnia* in some
detail, failed to understand the nature of either sexual or parthenogenetic reproduction in these animals. Unaware that they practised parthenogenesis, he not only thought that it was ‘clearly ascertained’ that a single copulation was sufficient to fecundate a female for life, but that it did so for all its female descendants for several successive generations. His opinion was based partly on the knowledge that, without seeing a male, Schäffer had reared four successive, as we now know, parthenogenetic, generations! Moreover, he believed that young emerging from ephippial (resting) eggs, always female, had also been fecundated by this one act of mating and could thereby produce offspring, and that their young could also do so without the intervention of a male—as indeed they can, but not for the reason he believed.

A glimmer of understanding of the basic differences between parthenogenetic and sexual reproduction in *Daphnia* was not to be achieved until 1857, when John Lubbock—later more famous in other spheres as Lord Avebury FRS—clarified the distinction in a paper communicated to *Philosophical Transactions* by Charles Darwin. These modes of reproduction are now well known, but *Daphnia* continues to surprise us. For example, some species have races of obligate parthenogens, and males that can act as carriers of the gene for asexuality—a discovery that would have delighted Schäffer.

Although Schäffer gave an accurate account of the general habits of *D. magna*, some points were criticized 65 years later by his worthy successor Louis Jurine, who, other than De Geer, was the first of subsequent investigators to provide significant information on the structure and habits of *Daphnia* and its allies. This he did in a splendid monograph that dealt with a wide range of microscopic crustaceans. By this time, systematic studies on these tiny animals had begun and were vigorously prosecuted, especially by Otto Friderich Müller, but of Schäffer’s successors it was Jurine who first paid similar attention to morphological details. He records how he had long sought a copy of the latter’s work and had lost all hope of doing so when, his own work complete, he acquired one. When he saw that Schäffer dealt largely with a species different from that studied by himself, he decided to publish his own text as it stood and, as an appendix, added a translation into French, made by a friend, of parts of Schäffer’s work, with comments where they seemed appropriate. For example he criticized the latter’s account of how *D. magna* repeatedly pushes its head against the bottom or other objects in quest of food, and somewhat condescendingly remarked that he appeared to forget that *Daphnia* always bounces up and down in the water without ever going to the bottom and without the need to go there in search of food. Jurine, however, failed to realize the significance of the fact that Schäffer’s animal was not the same as that which he described in his own monograph as *Monoculus* (=*Daphnia*) *pulex*, and made the erroneous assumption that all species of *Daphnia* behave in a similar manner. In fact different species differ greatly in habits and ecological preferences. Although *D. magna*, with which Schäffer was concerned, often swims in open water, it also scrambles among bottom detritus, where it collects food. Jurine also gave the misleading impression that Schäffer regarded *D. magna* as a carnivore by saying that it gives chase to the insects which serve as food (*pour donner la chasse aux insectes qui servent à sa subsistance*). However, Schäffer, who, as was then the custom, used ‘insects’ as a blanket term for what he clearly intended to mean minute organisms, says nothing about ‘giving chase’ but refers merely to obtaining needful insects or other kinds of food that serve as sustenance. As his description of food collection—one of the most remarkable parts of his account—makes plain, there is no suggestion of ‘giving chase’ to prey of any kind.

The superiority of Schäffer’s observations on anatomy and function over some of those made much later is also nicely demonstrated by considering what Jurine regarded as defects in his account. These in fact revealed shortcomings in his own understanding, although his work
as a whole was highly meritorious. For example, rightly claiming that the carapace has no hinge, he doubted Schäffer’s statement that Daphnia had the ability to adjust the width of the gap between its two valves. Schäffer was correct. Jurine was evidently unaware that, although the carapace is continuous dorsally, its two valves are united by a pair of adductor muscles—shown as A and P just behind, and to the right of, the mandible in figure 6—and is sufficiently flexible to permit the movements described by Schäffer. He also claimed that Schäffer had not been able to distinguish what constitutes the cerebral ganglion (‘brain’). The latter, however, did so very accurately and it was Jurine who gave a confused account. Schäffer not only noted the conspicuous optic lobe (labelled 3 in his Plate II, Fig. II, but also another, labelled 2) that extended towards the ocellus, which led him to identify that small black spot correctly as a simple eye. These lobes, as portrayed by Schäffer, can be compared with a late twentieth-century illustration (of a different species) in figure 6. The muscles that roll the eye are omitted in the latter. The ocellus was not seen by Jurine in what he called Monoculus pulex—whose identity is uncertain. Schäffer also observed the nerves to the antennules, deduced correctly to be organs of touch or taste. Jurine’s account of these features was confused. However, he deserves much credit for his independent observation of the inflowing, food-carrying current. He also saw food moving forwards along the food groove, but incorrectly believed that the current changed direction at the posterior end of the groove and flowed forwards, and specifically referred to the liquid and the food particles that it contains as flowing towards the mandibles. The current in fact leaves the carapace chamber posteriorly and food is swept along the food groove by mechanical means. Not surprisingly, Schäffer did make mistakes. He believed that two ducts ran alongside the alimentary canal. As no such ducts exist, his speculation as to their function was groundless, and Jurine’s criticism was justified.

Schäffer’s observations on the relation of structure to function in anostracans and notostracans were also the first ever made on either of these two groups of branchiopods. He was also the first to observe the hatching of a resting egg of Triops and the nauplius larva that emerged from it. Ironically, although his work on these animals has been largely forgotten, two of his illustrations of Triops, published in 1756, found their way into textbooks, have been repeatedly used, and appear there still. Their most recent use seems to be in the 1970 English edition of a German textbook of 1967! Their survival for more than 200 years, not as historical relics but as contemporary aids to understanding, is a fitting monument to the carcinological work of this remarkable man.

ACKNOWLEDGEMENTS

The portrait of Schäffer is reproduced from an image provided by Fürst Thurn und Taxis, Regensburg. I thank Dr Rony Huys and Dr Geoffrey Boxshall, who pursued, or enabled me to consult, old literature at the Natural History Museum, London; Martin Carr of the Royal Society Library, for helpful information; Jennifer Kren for checking the illustrations in Joblot 1718; and my old friend Eric Hollowday, who assures me that the Brachionus that occurs commensally on pond-frequenting European Daphnia is invariably B. rubens.

NOTES

9 A. Trembley, *Mémoires, pour servir à l’histoire d’un genre de polypes d’eau douce à bras en forme de cornes* (Jean & Herman Verbeek, Leiden, 1744).
13 L. Joblot, *Observations d’Histoire Naturelle, faites avec la Microscope* (Paris, 1754). Joblot died in 1723. This is a long-posthumous revision of his book *Descriptions et usages de plusieurs nouveaux microscopes, tant simples que composez* (Collombat, Paris, 1718), in which there is no such illustration.
19 J. C. Schäffer (as Schaeffer), *Apus pisciformis insecti aquatici species noviter detecta brevibusque descripta* (Norimbergae, 1752).
20 J. C. Schäffer, *Die fischförmige Kiefenfuss in stehenden Wassern um Regensburg* (Regensburg, 1756).
21 J. C. Schäffer, *Der krebsartige Kiefenfuss mit der kurzen und langen Schwanzklappe* (Ratisbon, 1756).
26 In 1861 Georg Ossian Sars produced a historically important manuscript that included good pencil drawings of isolated limbs of a *Daphnia* of uncertain identity. This, translated into English from the original Norwegian, was eventually published in 1993 by the University of Bergen under the title ‘On the freshwater crustaceans occurring in the vicinity of Christiania’.
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<td>O. F. Müller</td>
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