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DIGESTICHNIA (VIALOV, 1972) – AN ALMOST FORGOTTEN ETHOLOGICAL CLASS FOR TRACE FOSSILS

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Abstract—The new ethological class Digestichnia is introduced in the present article. It comprises all trace fossils (and their recent counterparts) originating from the digestive process of animals, such as coprolites (feces), regurgitalites (regurgitations) and gastroliths. The class is based upon a group within the unused classification system for trace fossils proposed by Vialov in 1972.

INTRODUCTION

For coprolites of all kinds (including cololites *sensu* Hunt, 1992), the ethological class Faecichnia was informally introduced in the 'Skolithos'-Internet-forum in 2002 (e.g., http://listserv.rediris.es/cgi-bin/wa?A2=ind0211&L=SKOLITHOS&F=&S=&P=5116). This term obviously was created by several parties independent of each other, but was never formally erected (M. Bertling, personal commun., 2010). Recently, the term was utilized by Patel and Desai (2009), who introduced the Faecichnia-ichnocoenosis for pellet-dominated environments that were produced by the reworking of the surface layers of matgrounds by crustaceans and polychaetes in sand-dominated tidal areas.

In any case, the term Faecichnia unfortunately does not encompass all the processes that may occur during digestion. Hence, regurgitations and gastroliths are not covered by this term, and its use as an ethological class is therefore not recommended. However, Vialov (1972) introduced the class-like category "Digestisignia," comprising all kinds of traces left by digestion, including feces, regurgitations and gastroliths. Unfortunately, his system of trace fossil classification was too detailed (see below) and therefore rather impractical, which is why it was neither taken over by Western nor Eastern scientists. Thus, the term has not been used in the last few decades. The following article draws attention to this forgotten class-like category by providing it with a proper definition, and by renaming it according to modern standards as Digestichnia (after Seilacher, 1953; cf. Bromley, 1996).

THE CLASSIFICATION SYSTEM OF VIALOV (1972)

The first comprehensive classification system for trace fossils was presented by Seilacher in 1953, who divided trace fossils according to the behavior of the tracemaker at the moment the trace was created. Nowadays, his system of ethological classes is widely accepted. Several authors tried to extend this system by adding or dividing classes (e.g., Müller, 1962). However, most of these classes or class-subdivisions were not accepted in the years following their publication. The latest published scheme for animal behavior by Bromley (1996) has seven ethological classes in addition to the original five given by Seilacher (1953). Later additions to that scheme are the Fixichnia by Gibert et al. (2004) for attachment traces and, more recently, the Mortichnia by Seilacher (2007) for traces that were produced during a death struggle.

In 1972, Vialov published a detailed classification system for trace fossils, mainly as an extension of the Seilacherian system. In contrast to the much more practical ethological approach by Seilacher (1953), Vialov (1972) distinguished between "Vivichnia" and "Vivisignia." He defined his "Vivichnia" as "physical traces left by the body or extremities of the [living] animal" and his "Vivisignia" as "traces, or more precisely, signs [and their remains] of physiological activity" by an animal. Further subdivisions were made for these two categories according to the tracemaker's taxonomy (vertebrates or invertebrates), and the purpose of the trace or the tracemaker's behavior while producing it. In the fossil record these criteria are not always determinable, so many trace fossils could not be placed in Vialov's system.

Translated into the ethological system based on Seilacher (1953), the "Vivichnia" sensu Vialov (1972) mainly comprise Repichnia (including all movement traces), Aedificichnia and Domichnia. The "Vivisignia" on the other hand, include all kinds of traces produced by the body functions of the tracemaker. Most of these "Vivisignia" categories (signs of growth, illnesses and injuries) were later excluded from consideration as trace fossils by Bertling et al. (2006). However, the class-like category of the "Digestisignia" matches the requirements for trace fossils given by Bertling et al. (2006) and is characterized and renamed in the following as the ethological class "Digestichnia" to be etymologically consistent with the Seilacherian system.

DIGESTICHNIA (VIALOV, 1972)

The above mentioned complexity, impracticality and the fact that Vialov failed to publish it in a widely distributed journal (it was only published as a conference abstract) led to the classification system being essentially ignored and eventually being buried in oblivion. Nevertheless, traces of digestion are common in the fossil record in terrestrial as well as in marine environments (see this volume) and have to be included in the widely accepted system of animal behavior based on Seilacher (1953).

Regardless whether produced by invertebrates or vertebrates, fossil remains from the digestive systems, such as coprolites (including cololites), regurgitalites, gastroliths, etc. have to be regarded as trace fossils (cf. Abel, 1935; Hunt, 1992; Bertling et al., 2006). Following Bertling et al. (2006), trace fossils are morphologically reoccurring structures that result from the live activity of an individual organism or homotypic organisms modifying a substrate. For coprolites and regurgitalites the modified substrate consists of more or less (semi-) digested food and food parts (cf. Bertling et al., 2006). Gastroliths, on the other hand, are substrate stones or stone-like concretions that have been modified by in-stomach digestive action and therefore show abrasion and etching caused by rhythmic muscular contractions of the gizzard, stomach acids and enzymes (cf. Bertling et al., 2006, cf. Wings, 2004, 2007). It is not important in this context whether these stones are ingested deliberately or accidentally by the tracemaker or whether they were generated inside the digestive organs (see below for discussion and explanation).

Coprolites of vertebrate or invertebrate origin (e.g., fecal pellets of molluscs, brachiopods or arthropods) as well as other excretions leaving the intestines at the distal end of an organism would be covered by the informally introduced term Faecichnia (Skolithos-Internet-forum on trace fossils: http://listserv.rediris.es/archives/skolithos.html 2002). But digestion is much more complex. Especially, reptiles, birds and some fish, but also some molluscs (e.g., cephalopods, suspension-feeding pelecypods and gastropods) regurgitate undigestible parts such as bones, scales, hair or parts of exoskeletons of their prey or accidentally ingested sediment particles (e.g., Petzold, 1959, 1967; Schäfer, 1962; Duke et al., 1976; Andrews, 1990; Hockett, 1996; Bochenski et al., 1993; 1998; Prins et al., 1991).

Documentation or scientific research on regurgitations of groups other than birds is very scarce. However, on the basis of the published literature and the examples from the fossil record, a definition of regurgitations produced by vertebrates can be attempted: Fossil and Recent vertebrate regurgitations are accumulations of disarticulated or partly articulated, indigestible parts of prey animals (rarely also plants or fungi), sometimes of various origins. These accumulations very often exhibit a sharp boundary towards the surrounding sediment, which was caused by the adhesive organic slime binding together the indigestible, regurgitated parts.

Hard content, like bones or (parts of) exoskeletons, can be partly fractured due to chewing and biting (Fig. 1) or dissolution by stomach acids by the predator (Bochenski et al., 1993, 1998 and references to different birds therein); it may also remain completely intact when the prey was swallowed as one piece. In contrast to hard body parts found in coprolites (cf. Fisher, 1981; Andrews and Fernández-Jalvo, 1998), regurgitated material is bigger in size and articulated hard body parts occur more often (Fig. 2; cf. Sanz et al., 2001). Fractured and unfractured content of regurgitalites may show signs of etching by stomach-acids like surface pitting (Hockett, 1996; Sanz et al., 2001). Especially, around holes or fractures, the bone tissue is very often thinned out and the edges are rounded (Bochenski et al., 1993, 1998; Hockett, 1996). The articular ends of bones are often corroded (Sanz et al., 2001). Digestive enzymes and stomach acids can further cause polishing and staining of bones (Hockett, 1996 and references herein) as well as exfoliation (Andrews, 1990). These stomach fluids and additional mucus ease regurgitation of the indigestible material and bind together the more or less loose parts. Even when regurgitated higher up in the water column this slime probably gives the regurgitation considerable cohesion and prevents the hard parts from being scattered widely over the sea or lake floor. The lack of any fecal matrix (Sanz et al., 2001) provides an additional criterion to identify (fossil) regurgitalites. Observations of various pellet-casting birds resulted in a large number of factors controlling the physical aspect of regurgitations, especially the etching patterns on hard body parts (cf. Hockett, 1996). As an example, such factors may be the time interval between swallowing and regurgitation (Duke et al., 1976), the pH of the stomach solution (Duke et al., 1975) or the power of digestive enzymes (Hockett, 1996). These factors will most likely also be present in other groups than birds and impact the aspect of the regurgitated material.

Fossil regurgitalites are especially known from calm-water environments, where their preservation potential is high. Regurgitations thus are known from the Lower Jurassic Posidonia Shales of Holzmaden (Fig. 2; Keller, 1977; Böttcher, 1989, 1990), the Upper Jurassic Lithographic Limestones of Solnhofen (Janicke, 1970; Barthel and Janicke, 1970) and Nusplingen in southern Germany (Fig. 1; Schweigert et al., 2001) or the Early Cretaceous Las Hoyas lacustrine limestones in Spain (Sanz et al., 2001), to cite a few examples.

Regurgitations of invertebrates are mainly referred to as pseudofeces. Suspension-feeding molluscs gather food by filtering suspended particles out of the water with their gills. Mucus binds these particles and then they are transported to the palps beside the mouth where they are sorted for edibleness. Those particles found inedible are further bound in mucus and expelled from the system as pseudofeces. Mucus-binding is essential for efficient ejection and allows these pellets to survive as sand-sized sediment grains for some time. These regurgitated mucus-bound pellets resemble feces quite closely, differing only in not having passed through the bivalve's gut (e.g., Prins et al., 1991 and references herein). In the fossil record, they therefore might be misidentified as coprolites. Criteria to distinguish pseudofeces from real fecal pellets seem not to have been studied, yet (Prins et al., 1991).

Gastroliths, stomach stones or gizzard stones also show signs of etching by stomach acids. Remaining within the stomach or rumen (or similar) longer than regurgitated material, they show additional abrasion and may sometimes be highly polished (Wings, 2003). Wings (2004) made experiments in artificial stomachs in order to find criteria for distinguishing gastroliths from isolated exotic pebbles. According to his experiments, polishing of the stones within the gizzard does not take place and therefore has to occur after the death of the gastrolith-bearing animal. Additionally, Schmeisser and Flood (2008) showed that geogastroliths very often show subparallel grooves on the etched surfaces.

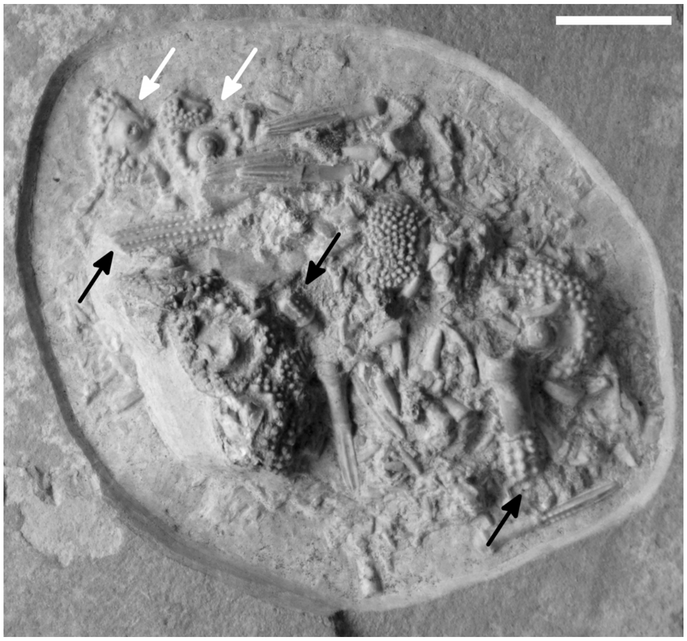

FIGURE 1. Regurgitated *Plegiocidaris crucifer* (Agassiz), SMNS 65411. The echinoid crushed by the teeth of the predator is clearly visible by its incomplete spines (black arrows) and skeletal ossicles (white arrows). The echinoid fragments were probably held together by mucus that eased the regurgitation process for the predator and increased the preservation potential as a regurgitalite. Nusplingen (SW-Germany), Upper Jurassic, Upper Kimmeridgian, Scale bar is 1 cm.

Gastroliths can perform several tasks. They occur regularly in several groups of vertebrates (e.g., archosaurs, pinnipeds) but also in invertebrates (e.g., crustaceans). A classification system and a redefinition for gastroliths was provided by Wings (2004, 2007). According to Wings (2004, 2007), gastroliths are hard objects of non-caloric value (stones, natural and pathological concretions) which are or were retained in the digestive tract of animals, and have a minimum diameter of 0.063 mm. Their external features, especially roundness and surface texture, strongly depend on the function of the stones. Additionally, other factors such as rock type, retention time or abrasion rate in the stomach influence the physical appearance of gastroliths.

Wings (2004, 2007) distinguishes between three different types of gastroliths: bio-gastroliths, patho-gastroliths and geo-gastroliths. This subdivision is based on the type of origin: Biogastroliths are non-pathological invertebrate concretions such as stomach concretions formed in arthropods. Especially some crustacean species reabsorb calcium from their old cuticle and store it in the form of gastrolithic concretions for later reuse after their ecdysis (Scheer, 1964). After moulting, these concretions are “digested” and the calcium is absorbed from the digestive tract, transported by blood and finally re-utilized for calcification of the new exoskeleton (e.g., Frizzell and Exline, 1958; Ueno et al., 1992). Due to their origin and the fact that no substrate material has been modified in this group, biogastroliths are not included within the Digestichnia (cf. Bertling et al., 2006).

Pathogastroliths are stone-like concretions that are mainly generated in the stomachs of herbivorous mammals by swallowed and felted hair or plant fibers. Such “stones” are also called “bezoar stones,” due to their abundance in stomachs of the bezoar goat (e.g., Elgood, 1935). Following Bertling et al. (2006), the felted hair and plant fibers have to be regarded as substrate modification. Pathogastroliths therefore are included within the Digestichnia.

Finally, Wings (2004, 2007) defined his geogastrolith as swal-

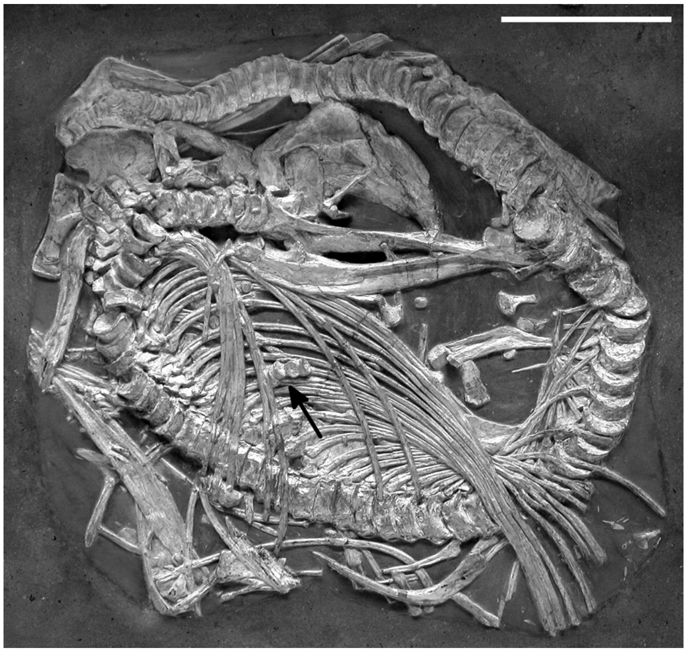

FIGURE 2. A small ichthyosaur (cf. *Stenopterygius quadrissicus*) as a possible regurgitalite of a larger ichthyosaur (discussion in Keller 1977), SMNS 15194. The isolated ribs and vertebrae inside (arrow) the curled ichthyosaur belonging to this skeleton, the lack of the smallest caudal vertebrae as well as the extreme torsion of the body all mark it as a regurgitalite. Due to the rather rough preparation (chipping) of this specimen, surface pitting (cf. Hockett, 1996; cf. Sanz et al., 2001) might not be preserved. Holzmaden (SW-Germany), Lower Jurassic, Toarcian, Scale bar is 10 cm.

lowed pebbles and sand (the term "grit" is used for smaller geogastrolith grain sizes in the range of sand with a minimum diameter of 0.63mm in birds). When these rock grains are deposited in a gizzard (muscular stomach used for grinding food particles), "gizzard stones" can therefore be used as a synonym. Another rather rarely used term for geogastroliths is "belly boulders."

For isolated exotic rocks discovered in fine-grained sediments, Wings (2004, 2007) introduced the term "exoliths." These may show a high polish and potentially (but not necessarily) might have been former gastroliths.

Geogastroliths, or more precisely, the modifications on their surfaces (like etchings and abrasion) have to be regarded as trace fossils according to Bertling et al. (2006). For exoliths, their origin from an animal's digestive organ needs to be proven beyond reasonable doubt. Criteria for the recognition of gastroliths isolated from any animal remains were published by Weems et al. (2007) and Schmeisser and Flood (2008) and do not need to be repeated here. However, their studies were restricted to gastroliths originating from larger vertebrates.

POSSIBLE ICHNOTAXOBASES FOR DIGESTICHNIA

In order to name trace fossils, ichnotaxobases need to be defined (Bertling et al., 2006). According to Fürsich (1974) and Bertling et al. (2006), highly significant behavior reflected in trace fossils should be used to distinguish trace fossils at ichnogeneric level and less significant behavior for ichnospecific determination. Bertling et al. (2006) compiled and discussed several commonly used characteristics in distinguishing trace fossils, from which not all are suitable for the Digestichnia. Up to now, not many ichnotaxa have been erected for Digestichnia, when compared to other trace fossils. The following list of ichnotaxobases is based on extant ichnotaxa for Digestichnia and will probably be extended in the future. It should only be used as a rough guideline and as a basis for further discussion.

Gastroliths

From the three major groups of Digestichnia (coprolites/feces, regurgitalites and gastroliths), the gastroliths provide the least characteristics that could be used as ichnotaxobases. Gastroliths are also the group of Digestichnia that is least understood and most rarely investigated in detail (Wings, 2004, 2007; Weems et al., 2007; Schmeisser and Flood, 2008). So far, no ichnotaxon has been erected for gastroliths.

Although pathogastroliths might not be preserved in the fossil record, they should be distinguished from geogastroliths at the ichnogeneric, if not an even higher, level. The felting of plant fibers and/or hairs inside the stomach into pebble-like pathogastroliths clearly differs from the behavior reflected by geogastroliths (see above). Principal composition, arrangement of components as well as their size distribution may provide ichnotaxobases here.

According to Wings (2004, 2007), the grain size of the geogastroliths is highly variable and is therefore not a suitable ichnotaxobase. This is because the interaction of anatomical, ontogenetic and geographic factors can hardly be resolved: The grainsizes contained in the gizzard depend on the maximum size that can be swallowed and comfortably passed through the esophagus of the tracemaker. Their minimum size reflects the diameter of the distal exit of the gizzard (cf. Wings, 2004). Gastroliths recovered from the bowels therefore should be smaller or have the same size as the smallest gastroliths within the gizzard. On the other hand, gizzards of large tracemakers can contain geogastroliths with larger diameters than the gizzards of smaller tracemakers. The range between maximum and minimum grain size may therefore be wider in larger tracemakers than it is in smaller ones. But, during ontogeny, this size range of geogastroliths will increase according to the body size of the tracemaker.

Finally, the type of substrate rocks theoretically may seem to be a useful ichnotaxobase at the ichnospecies level. Wings (2004) showed that some ostriches prefer rocks of certain sizes and colors. On the other hand, he also states that the real "selection" occurs in the gizzard. Soft rocks are quickly eroded and carbonates become dissolved, leaving mainly the most durable rock types, such as quartz varieties and quartzitic rocks (Wings, 2004; Wings and Sander, 2007). In addition, rock types available in the living space of the tracemakers will limit their choices. Based on these considerations, prevailing rock types will not be useful ichotaxobases in praxis.

Possible ichnotaxobases for geogastroliths may be found on closer inspection of the surface microstructures. The study of Schmeisser and Flood (2008), however, suggests that they strongly depend on the composition, texture and structure of the host rock, pointing to the necessity of future research into this issue.

Regurgitalites

No ichnotaxon has been established for regurgitalites to date. The size and shape of any regurgitated mass depends on the food it was derived from. Indigestible content may be held together by felted plant fibers, hair or feathers and/or mucus to form a pellet (e.g., Fitch et al., 1946) or may have a more amorphous outline. Depending on the sedimentary environment and the amount of slime adhesive to the indigestible food particles, these regurgitalites may lie together on a spot (mainly bird pellets, but also in marine environments, cf. Schweigert et al., 2001) or might be scattered over a certain area (e.g., Dietl and Schweigert, 2001). Modern pellets of diurnal birds of prey and owls differ from each other in shape, as well as in type, size range and arrangement of their components. In modern owls and birds of prey, prey is usually swallowed in one piece, but some (e.g. *Glaucidium passerinum* and *Buteo jamaicensis*) break bones of prey animals with their beaks (Fitch et al., 1946; Mebs and Scherzinger, 2000) and eat their prey in small pieces. Depending on the time between ingestion and regurgitation and the strength of the digestive liquids, hard body parts show different stages of corrosion. The intactness of hard parts of the prey combined with the overall shape and size of the regurgitation could therefore be used at the ichnogeneric level. The content might vary due to different diets during the seasons, however (e.g., more insect-rich in summer), and might be better used at ichnospecific level.

Invertebrate regurgitations are hardly known as yet. The difficulty to distinguish between pseudofeces and real feces further complicates the matter. Suggestions for possible ichnotaxobases of invertebrate regurgitalites can therefore not be given to date.

Coprolites

The distinctive and reoccurring patterns of coprolites of invertebrate and vertebrate origin have been recognized early, thus a number of (mainly monospecific) ichnogenera already exists (e.g., Häntzschel, 1975; Hunt et al., 1998). Hunt and Lucas (2010) listed and discussed criteria that can be used for assigning vertebrate coprolites to their tracemakers. Most of these criteria are also helpful in describing feces and coprolites and therefore could be used as ichnotaxobases. The ones suitable as ichnotaxobases for both invertebrate and vertebrate feces/coprolites are listed and discussed in the following.

Although absolute size is not recommended as an ichnotaxobase by Bertling et al. (2006) for the majority of trace fossils, some vertebrate and invertebrate feces (especially fecal pellets from e.g., rodents, and bats or invertebrate microcoprolites, e.g., Favreinidae) exhibit a very narrow size range (e.g., Häntzschel, 1975; Schweigert et al., 1997; Strachan, 2010). For the majority of feces (other than fecal pellets), however, size is not a useful ichnotaxobase.

External shape has been used to distinguish coprolite ichnogenera and ichnospecies. Just as for any other trace fossils, shape-defining ratios of e.g., length to width or diameter are good ichnotaxobases for coprolites of invertebrate and vertebrate tracemakers (e.g., Hunt et al., 2005b, 2007). Not only the overall shape of coprolites but also their surface texture (e.g., smooth, striations, incisions, etc.) or whether they are built up out of concavo-convex subunits (cf. Milàn and Hedegaard, 2010) can be used to define ichnogenera or -species. An overview of the most abundant coprolite shapes was given by Häntzschel et al. (1968). Some of the external shapes illustrated by Häntzschel et al. (1968) might also be useful in defining ichnotaxa for pellet-shaped regurgitations.

Especially in microcoprolites, the internal structure (e.g., number, shape and arrangement of internal canals) is used to define both ichnogenus and -species (Vialov, 1978; Schweigert et al., 1997 and further references therein; Senowbari-Daryan and Kube, 2003 and further references therein). Internal structures are also observed in vertebrate macrocoprolites (Hunt et al., 2005a, cf. also Schweigert, this volume), which are used to define ichnotaxa.

A carnivore, herbivore or omnivore diet is reflected in the content of coprolites (Thulborn, 1991). Due to preservational bias (Hunt et al., 1994), the fossil record of herbivore coprolites is much sparser than of carnivore feces. Phosphatically preserved coprolites are usually assigned to carnivore tracemakers (Hunt et al., 1994; Hunt and Lucas, 2010). Different diets reflect an important animal behavior and therefore are useful high-level ichnotaxobases in most cases. However, in omnivores, the diet may change seasonally according to available food sources.

When hard body parts of the prey animals are not regurgitated but passed through the digestive system, the strength of the predator's digestive liquids will have different impact on the corrosion of ingested bones and teeth. As an example, coprolites bearing teeth without enamel are believed to derive from crocodilian tracemakers (e.g. Hunt and Lucas, 2010 and further references therein).

Summarizing, it is very difficult to define ichnotaxobases for Digestichnia other than coprolites. Differing from all other ethological classes, the overall appearance of Digestichnia is influenced by a variety of parameters such as diet, strength of digestive liquids, etc. A combination of all available parameters should therefore be used to distinguish ichnogenera. For the distinction at ichnospecies level, recurring variations in these parameters may be used.

CONCLUSIONS

The new ethological class Digestichnia (originally proposed by Vialov, 1972) is introduced. The class Digestichnia is suggested to include all trace fossils (and Recent equivalents) produced by the digestive process, which are two out of three types of gastroliths (geo- and pathogastroliths sensu Wings, 2004, 2007), regurgitalites and coprolites/feces. Any material of non-caloric value leaving the digestive tract of the tracemaker in either way has to be regarded as a digestion trace (cf. Bertling et al., 2006) and is therefore included within the new ethological class Digestichnia. However, in the fossil record, individual bones or other hard body parts preserved within Digestichnia may in addition still be regarded as body fossils and treated as such. The trace fossil is made up by the accumulation of undigested material deriving from the digestive organs.

A combination of all available data is proposed as ichnotaxobases at the ichnogeneric level. At the ichnospecific level, recurring variations in these criteria should be used.

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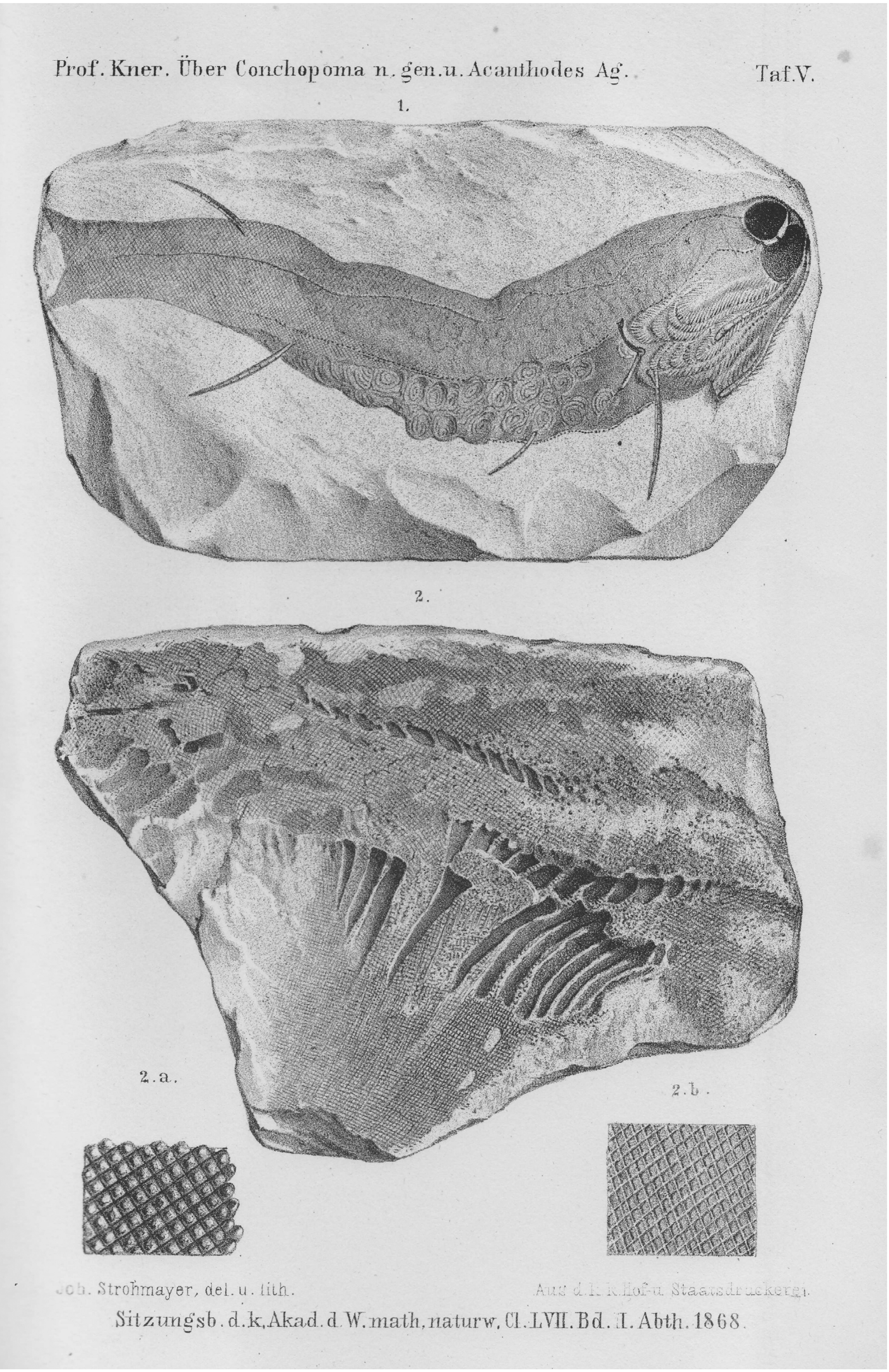

Prof. Kner. Über Conchopoma n. gen. u. Acanthodes Ag. Taf. V.

Joh. Strohmayer, del. u. lith.

Aus d. k. k. Hof- u. Staatsdruckerei.

Sitzungsb. d. k. Akad. d. W. math. naturw. Cl. LVII. Bd. I. Abth. 1868.

An acanthodian fish with conchostracans in the digestive system (from Kner).