Figure 1. | *Muschelkalk slab with three specimens of* Eosemionotus. *Collection: H. Winkelhorst.*

The fish fauna of the Winterswijk Vossenveld Formation

U vindt een samenvatting aan het eind van de tekst / You will find an abstract at the end of the text.

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In the past four to five decades, the Vossenveld Formation exposed in the Winterswijk Muschelkalk quarry has proven to be a treasure trove for research on marine vertebrates from the Anisian. To this day, fish fossils remained largely in the shadow of significant finds of sea reptile remains that received full attention over the years. Due to specific environmental circumstances, the number of fish species that lived in this part of the Muschelkalk Sea seems to be relatively limited. However, different genera were identified as soon as the collected fossils were systematically studied for the first time. And since the publication of the noteworthy article on the fish of the Winterswijk Muschelkalk by Oosterink and Poppe (1979), some additional species have been discovered. Here, we attempt to provide a complete overview of the species of fish that have been identified from the Winterswijk Vossenveld Formation to date.

The Winterswijk Muschelkalk (Vossenveld Formation) is deposited in a shallow inland sea at the western margins of the Germanic Basin. Presumably, it was a lagoon-like coastal area, some distance from the deeper parts of the Muschelkalk Sea. During the Anisian, there was a connection by a single narrow passage in the east with the Tethys Ocean, the ocean that was enclosed on three sides by the landmasses of the supercontinent Pangea. The Tethys in its turn was connected with the huge Panthalassa Ocean, roughly 8000 kilometers to the east.

The depositional environment of the Vossenveld Formation was a coastal plain with varying water levels and a seafloor of fine calcareous silt that regularly fell dry

completely. The climate was warm and arid, resulting in high water temperatures and presumably also a high salinity. For the local fish fauna, it was an ecosystem with certain constraints. For instance, there was a limited supply of food in the periods when this part of the Muschelkalk Sea frequently fell dry. When, after a dry period, the water returned, fish and other swimming organisms also came back, but life in and on the bottom (the benthic zone) was greatly reduced by the preceding drought. In the fine, virtually undisturbed lamination of the sediments of these periods, evidence for this nutrient-poor situation is found. The high salinity (possibly hypersaline environment) may also have led to relatively nutrient-poor conditions. This may be one of the reasons for the usually small dimensions of the fish found in the Winterswijk Muschelkalk. Another reason for this is the shallow, relatively sheltered coastal water that constituted a favorable habitat for small fish species and juvenile fishes.

Evolution and taxonomy

The origin of the fish, and therefore of all vertebrates (!), lies in the Cambrian (c. 540-485 MA= million years ago) when the first fishlike chordates (Chordata) appeared. Then followed a long period of about 100 million years in which the first superclass of vertebrates evolved; that of the jawless fish (Agnatha). Only in the Late Silurian (c. 425 MA) some classes of fish with jaws evolved, including those of the ray-finned fishes (Actinopterygii) and lobe-finned fishes (Sarcopterygii), both belonging to the very successful superclass of the bony fishes (Osteichthyes; see Cladogram, Figure 2. below). The subsequent Devonian (c. 420-358 MA) is also known as the 'Age of the fish'. During this period, a large diversification of the fish fauna took place in a relatively short time. In addition to the already mentioned bony fishes, the class of the cartilaginous fishes (Chondrichthyes) also arose and diversified in the Devonian. During the subsequent Carboniferous and Permian, most classes thrived; there was a rich, varied fish fauna.

During the mass extinction that marks the transition from the Permian to the Triassic (252 MA), a mere ~6 million years before the beginning of the Muschelkalk deposition, around 95% of all marine species became extinct worldwide. The number of fish species also decimated. Both classes of the bony fishes and the cartilaginous fishes persisted but were much impoverished in diversity due to the mass extinction. In contrast to the cartilaginous fishes, the diversity of bony fishes recovered well and relatively quickly during the Triassic. The bony fishes would eventually transcend all other classes of vertebrates in (species) number.

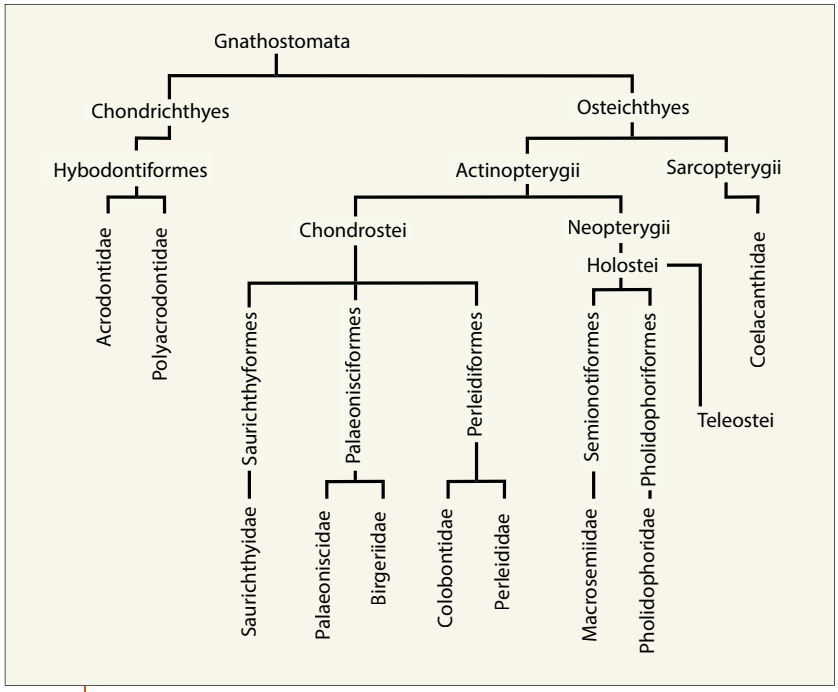

FIGURE 2. | *Simplified cladogram with the groups mentioned in this article.*

In consequence of the, on the geologic timescale, relatively short period after the Permian-Triassic mass extinction in which they were deposited, the Lower Muschelkalk deposits of Winterswijk give an insight into the 'recovery period' of, among others, the fishes. While considering the fact that local circumstances support a specific fish fauna that may differ from that of other localities, we observe that the bony fishes were significantly more abundant than cartilaginous fish in the Vossenveld Formation. There are several reasons for this observation: in the Triassic period cartilaginous fish were much less abundant than bony fishes, and, furthermore, the remnants of cartilaginous fish generally do not fossilize as well as those of bony fishes.

Chondrichthyes (Cartilaginous fishes)

Fossils of cartilaginous fishes (Chondrichthyes) are found in the Winterswijk Lower-Muschelkalk, albeit occasionally. So far, it only concerns teeth (Fig. 3A) and some sporadic fin spines (Fig. 3B) of sharks. The fossils found are attributed to two genera of hybodont sharks: *Acrodus* (Fig. 3) and *Palaeobates* (Fig. 4).

Acrodus
Order Hybodontiformes
Family: Acrodontidae
Genus: *Acrodus*

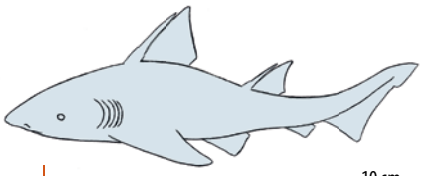

FIGURE 3. | Acrodus.

Characteristics: Body with the characteristic streamlined shape of sharks; an outspoken unevenly lobed (heterocercal) tail; two more or less triangular dorsal fins, each with a strong fin spine in front of the fin; a fairly broad mouth with approximately six rows of relatively low teeth with a corrugated, slightly elevated crown. Size: body length maximum approx. 2.5 m.

Lifestyle: On and near the bottom living shark with a durophagous feeding method. Diet: benthic organisms such as mollusks and crustaceans.

FIGURE 3AB. | *A:* Acrodus *tooth. Collection A. Haarhuis.*
B: Fin spine Acrodus. *Length approx. 7 cm. Collection J. van den Berg.*

Fossils: In Winterswijk, *Acrodus* teeth (Fig. 3A) of different sizes were found, ranging from approximately 0.5 cm to 2.5 cm in length. The variation depends not only on the size of the individual, but also on the original position of the teeth in the mouth. Dorsal fin spines (Fig. 3B), presumably from *Acrodus*) are sometimes found. These are slightly curved and have a surface with fine longitudinal ridges. The longest spine found measures as much as 20 cm (Oosterink, 2001).

Palaeobates
Order: Hybodontiformes
Family: Polyacrodontidae
Genus: *Palaeobates*

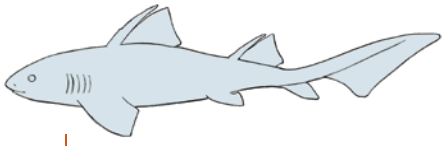

FIGURE 4. | Palaeobates.

Characteristics: Body probably largely similar to *Acrodus*; with two dorsal fins with a strong fin spine on the anterior margin; and a heterocercal tail (Fig. 4). The low-crowned teeth of *Palaeobates* (Fig. 4A) are much flatter than those of *Acrodus* (Fig. 3A) and have a dotted structure on the surface (upper side) instead of a striation. Size: body length approx. 1.0 m to 1.5 m.

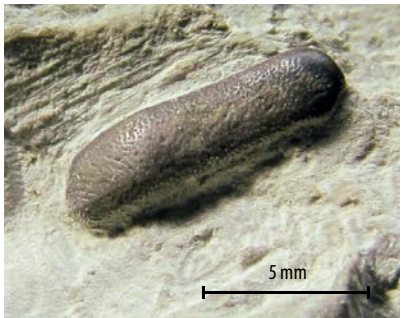

FIGURE 4A. | Palaeobates *tooth. Collection R. Bleeker.*

Lifestyle: On and near the bottom living shark with a durophagous feeding method. Diet: benthic organisms, probably mainly mollusks and crustaceans.

Fossils: In the Winterswijk Muschelkalk, teeth of *Palaeobates* (approx. 0.5 – 1.5 cm length) have been found, but these are significantly less abundant than the teeth of *Acrodus*.

Osteichthyes (Bony fishes)

Most fish fossils found in the Vossenveld Formation are remnants of bony fishes (Osteichthyes). From the Triassic up to the present, bony fishes are the most biodiverse and abundant class. Bony fishes are characterized by the ossification of the skeleton. During the Triassic, most of these fish also had a kind of exoskeleton, consisting of hard, firm ganoid scales. During the Triassic, representatives of several fish orders had only a sparingly ossified skeleton, but did have other characteristics of bony fishes. Therefore, a division between cartilaginous ganoids (Chondrostei) and bony ganoids (Holostei) is commonly used.

Chondrostei

Chondrostei form an infra-class of the Palaeopterygii. They are characterized by a skeleton consisting largely of cartilage, in combination with some typical osteichthyan characteristics. It is debatable whether they were still quite primitive in their development when compared to the bony ganoids. The relatively light cartilage skeleton actually offered several advantages. Some fish orders show an increase of cartilage at the expense of bone over time. However, Chondrostei also have some primitive characteristics. For instance, the ganoid scales of these cartilaginous ganoids are often thicker than those of bony ganoids, which yields a relatively stiff and heavy squamation. The lighter cartilage skeleton may have compensated for the weight of this. Also, most representatives of this group have a pronounced unevenly lobed (heterocercal) tail, as observed nowadays mainly in sharks. The genera described below all belong to the cartilaginous ganoids (Chondrostei).

Saurichthys
Order: Saurichthyiformes
Family: Saurichthyidae
Genus: *Saurichthys*
Species: *Saurichthys dianneae, Saurichthys* sp.

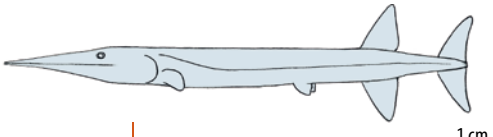

FIGURE 5. | Saurichthys.

Characteristics: Small to medium-sized fish with an elongated, streamlined body; long head with an elongated beak-like mouth; upper and lower jaw are equally

FIGURE 5AB. | *A:* Saurichthys. *Former Collection H. Oosterink.* *B:* Saurichthys, *posterior part. Collection G. Goris.*

FIGURE 6AB. | *A:* Gyrolepis. *Collection H. Winkelhorst.* *B:* Gyrolepis. *Collection R. Bleeker.*

long (Fig. 5). The dorsal fin is located very far towards the back and stands right above the anal fin. The tail is of the diphycercal type, whereby the uniform tail fin lobes are separated by the spine running straight to the posterior end. The squamation is limited to some (four) isolated longitudinal rows of scales. The teeth are relatively large, pointed and cone-shaped. Size: the adult body length of the species found in Winterswijk is approximately 10 to 25 cm. The head length is about one-third of the total body length. Elsewhere considerably larger specimens of the widely spread Saurichthyidae are found.

Lifestyle: *Saurichthys* is a pelagic predator that probably foraged in the entire water column. Presumably, it swam in schools. This certainly applies to the juveniles, given the discovery of a limestone slab with a concentration of remains of at least 18 young individuals in the Winterswijk quarry (Maxwell *et al.*, 2016). The slender body shape (Fig. 5A) also made it possible to hunt in very shallow water. The strongly posteriorly placed dorsal and anal fins, combined with the streamlined, torpedo-shaped body, enabled *Saurichthys* to catch prey through a very powerful acceleration, not unlike the modern pike. Food: especially small fish and other small, swimming organisms.

Fossils: A few *Saurichthys* fossils with a completely or partly preserved body (Fig. 5B) have been found in Winterswijk. However, the most common finds are either loose skulls or skull parts. Also, loose teeth can be found, but these are very small and difficult to distinguish from the teeth of certain other species, such as *Birgeria*.

Gyrolepis
Order: Palaeonisciformes
Family: Palaeoniscidae
Genus: *Gyrolepis*

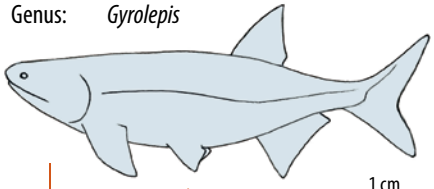

FIGURE 6. | Gyrolepis.

Characteristics: Small to medium-sized fish with a relatively slender, more or less fusiform body shape (Fig. 6);

a fairly long, slightly tapered and slightly upward inclined head with hefty jaws. The triangular dorsal fin is positioned slightly backwards; the front of the dorsal fin lies clearly before the front of the anal fin. *Gyrolepis* has a deeply forked, heterocercal tail. The thick, ganoid scales have a distinctive diamond shape, with a (ribbed) ganoid layer at the top and a central thickening at the bottom. The teeth are conical in shape. Size: the largest of the two Winterswijk specimens mentioned below had a total body length of almost 10 cm. Elsewhere in the Muschelkalk deposits specimens of more than 30 cm are known.

Lifestyle: Actively hunting predator. Food: small fish and small crustaceans.

Fossils: In the Vossenveld Formation of Winterswijk two beautiful, approximately three-quarter complete *Gyrolepis* specimens were found (see Figures 6A and 6B). Both specimens lack the posterior part and have (without the tail part) a length of 7 cm and 5 cm, respectively. Loose *Gyrolepis* scales are regularly found.

Birgeria
Order: Palaeonisciformes
Family: Birgeriidae
Genus: *Birgeria*

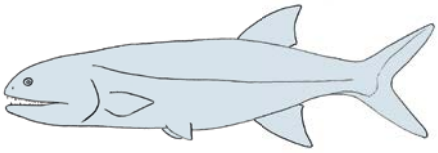

Figure 7. | Birgeria.

Characteristics: Large fish with a stretched, relatively slender body shape (Fig. 7). *Birgeria* has a long head with a slightly rounded snout and a large mouth. The triangular dorsal fin is positioned far to the back, at about the same height as the almost equally large anal fin. The pectoral and pelvic fins are proportionately smaller. *Birgeria* has a strong, almost symmetrical heterocercal tail. Squamation is characterized by small unobtrusive scales. Large conical teeth are located between a multitude of very small, mostly sharp teeth. Size: body length up to approx. 1 m.

Lifestyle: *Birgeria* was a large, pelagic predator, high up in the food chain.

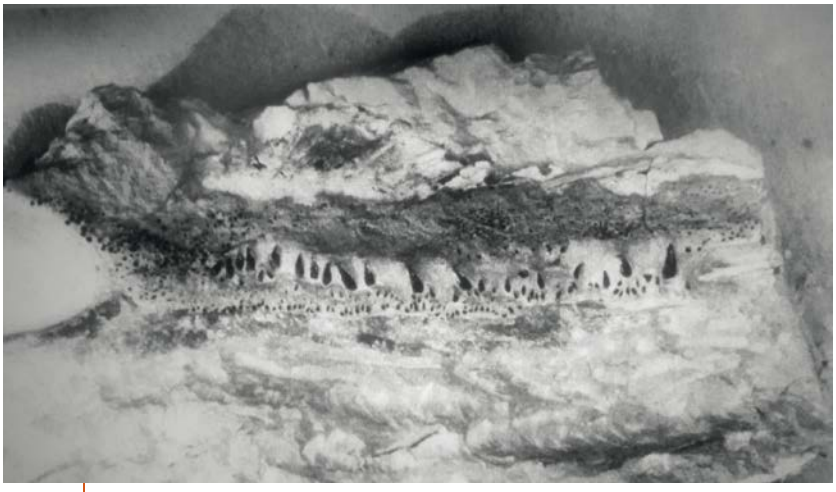

Figure 7a. | Birgeria *jaw. Scale uncertain. From: Oosterink & Diepenbroek, 1990.*

The shape of the body and the fin pattern reveal that it was a powerful swimmer that also felt at home in the open sea and probably hunted mainly in open water. Food: fish and cephalopods.

Fossils: This large predator would have been a rare appearance in the shallow coastal water in this part of the Muschelkalk Sea. The chance to find fossil remains in the Vossenveld Formation is therefore small. However, Oosterink and Diepenbroek (1990) published the find of a distinctive jaw (Fig. 7A) of *Birgeria* in the Winterswijk quarry.

Colobodus
Order: Perleidiformes
Family: Colobontidae
Genus: *Colobodus*

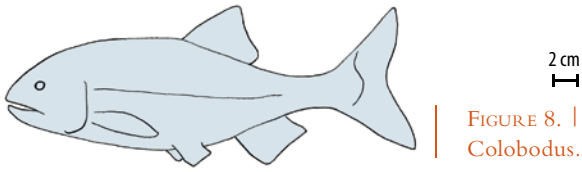

Figure 8. | Colobodus.

Characteristics: Medium-sized fish with a fairly sturdy build (Fig. 8). The head is relatively large, slightly tapered and it has a somewhat rounded snout. The onset of the dorsal fin lies behind the center of the body but clearly before the start of the anal fin. The caudal (tail) fin is (slightly) forked and practically even lobed. The hefty, thick, ganoid *Colobodus* scales are partly ornamented with more or less parallel ridges. The larger flank scales have indentations at the posterior end. The dentition shows conical teeth along the lateral side and tooth plates with numerous bullet-shaped teeth medially. Size: body length at most 50 to 70 cm.

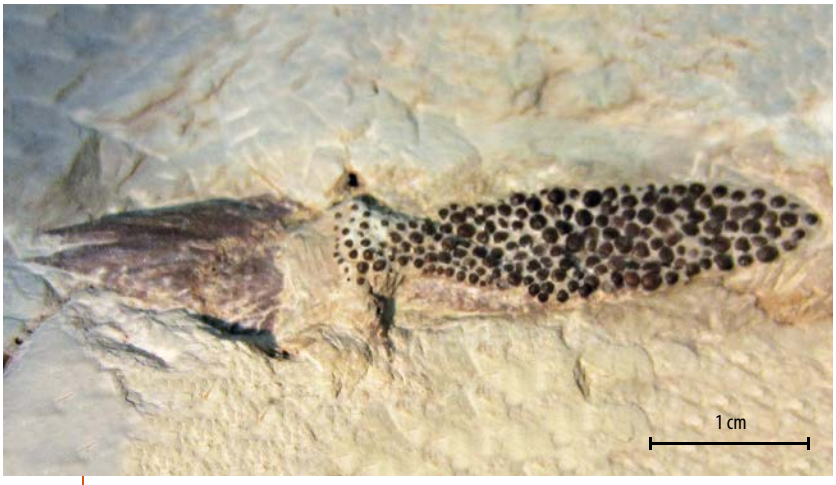

Figure 8a. | Colobodus *jaw fragment, with crushing teeth. Collection R. Bleeker.*

Lifestyle: Near the bottom living fish with a durophagous feeding method. Diet: benthic organisms, in particular crustaceans and mollusks.

Fossils: Tooth plates with small crushing teeth of *Colobodus* are regularly found in Winterswijk (Fig. 8A). A few times a larger (partly) articulated *Colobodus* specimen has been found. Many of the loose, larger, thick ganoid, sometimes partially articulated, scales that are found in the quarry belong to *Colobodus*.

Dollopterus
Order: Perleidiformes
Family: Perleididae / Colobontidae
Genus: *Dollopterus*

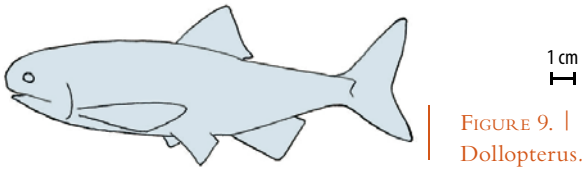

FIGURE 9. | Dollopterus.

Characteristics: Medium-sized fish with a stocky body shape (Fig. 9). *Dollopterus* has a rounded head with a fairly stump snout. The dorsal fin is positioned somewhat behind the center of the body, but the start of the fin lies clearly before the anal fin. The pectoral fins of *Dollopterus* are extremely large. The caudal fin is slightly heterocercal. The fish has thick scales with a smooth ganoid surface, and they show well-developed peg-and-socket connections; the flank scales have indentations on the posterior end. Crushing dentition, similar to *Colobodus*. Size: body length up to approx. 30 cm (considerably smaller than the related *Colobodus*). When the pectoral fins were spread, the 'wingspan' was about equal to the body length (!).

FIGURE 9AB. | *A:* Dollopterus *remains. Collection H. Winkelhorst. B:* Dollopterus *specimen. Collection TwentseWelle.*

Lifestyle: Fish living near the bottom with a durophagous feeding method. Diet: benthic organisms, in particular crustaceans and mollusks. Due to the very large pectoral fins, *Dollopterus* was often considered to be a flying fish. But given its physique, the heavy scales (Fig. 9A) and the lack of a large tail fin for the necessary thrust, that option is practically excluded. The broad pectoral fins could instead be used to move in a very controlled way on, or just above, the seafloor in search for food.

Fossils: Scales and dental plates of *Dollopterus* can be easily confused with those of *Colobodus*. Only a very few larger, more or less articulated remains of *Dollopterus* are known from the Winterswijk quarry (Fig. 9B).

Holostei

The bony ganoids (Holostei) are an infra-class of the Neopterygii, the group that also comprises the modern bony fishes (Teleostei). In the skeleton of the Holostei, and in particular in the spine, a certain degree of ossification occurs. Other developments take place in the structure of the skull, among other things enhancing the mobility of the jaws. The thickness of the ganoid scales decreases, resulting in a lighter and more flexible squamation. The tail gradually obtains a somewhat more even-lobed hemi-homocercal form. The two tail lobes are in most cases not yet entirely symmetric relative to each other; usually, the upper lobe is still slightly larger and the squamation covers a part of the upper lobe. The morphological characteristics of the bony ganoids provide these fish with a structure that already strongly resembles modern bony fishes (Teleostei). Two bony ganoids are known from Winterswijk: *Eosemionotus* (Fig. 10) and *Pholidophorus* (Fig. 11).

Eosemionotus

Order: Semionotiformes
Family: Macrosemiidae
Genus: *Eosemionotus*
Species: *Eosemionotus vogelii, Eosemionotus minutus*

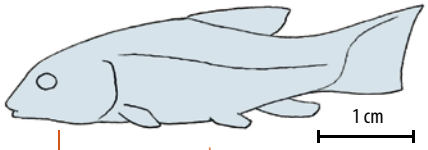

FIGURE 10. | Eosemionotus.

Characteristics: Small to very small fish with a slightly stocky, fusiform body. Relatively large head (length more than a quarter of the total body length). Small inferior mouth with a limited number of relatively long, conical teeth. The two halves of the frontal bone are completely fused. The dorsal fin with approx. 8 fin rays (the dorsal fin of *E. minutus* has 6 fin rays) begins roughly at the center of the body. The onset of the small pectoral fins lies ventrally right below the beginning of the dorsal fin. The anal fin has 6 to 8 fin rays. The heterocercal caudal fin is very lightly forked and has 12 to 14 fin rays. The smooth scales have a thin ganoid layer. The anterior flank scales are notably higher than the posterior flank scales. The squamation has less than 30 scales along the lateral line. On *E. vogelii,* the squamation continues onto the upper side of the caudal fin. Sizes: *E. vogelii* 4-5 cm; *E. minutus* approx. 3 cm.

Lifestyle: Shoal fish with a preference for shallow water in a near-coastal environment. *Eosemionotus* itself was regular prey for larger fish and predatory marine reptiles.

Fossils: *Eosemionotus* is by far the most common fish in the Vossenveld Formation. In general, species that are lower in the food chain have a higher population density. This is one of the reasons for the numerous representatives of smaller fish, especially *Eosemionotus*, in the fish fauna of the Winterswijk Muschelkalk. Another explanation is the specific local ecosystem, with predominantly (very) shallow water, possibly with sheltering conditions; an environment especially suitable for small and juvenile fish. Nearly complete fossils of two species have been found here; *Eosemionotus vogelii* (Fig. 10A, 10B & 10C) and the smaller *Eosemionotus minutus* (Fig. 10D) (Wijngaarden *et al.*, 2019).

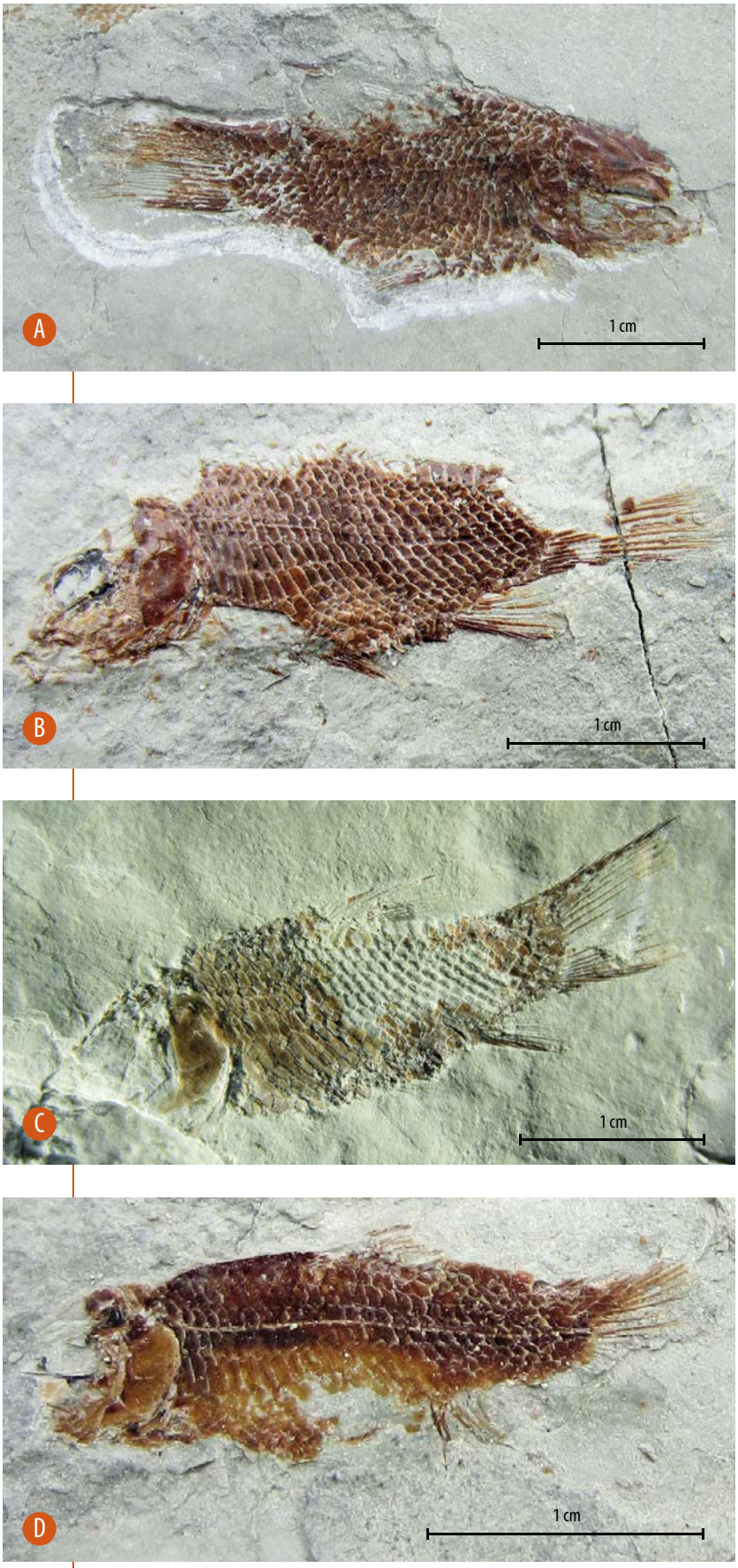

FIGURE 10 A-D. | *A:* Eosemionotus vogelii. *Collection H. Winkelhorst.*
B: Eosemionotus vogelii. *Collection H. Winkelhorst.*
C: Eosemionotus vogelii.
Collection Workgroup Muschelkalk Winterswijk.
D: Eosemionotus minutus. *Collection H. Winkelhorst.*

Pholidophorus
Order: Pholidophoriformes
Family: Pholidophoridae
Genus: *Pholidophorus*

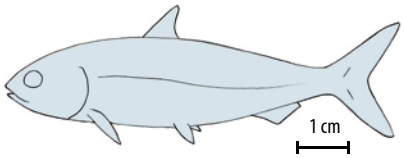

Figure 11. | Pholidophorus.

Characteristics: Small, slender fish with a streamlined, fusiform body (Fig. 11). The head is quite small (length approximately one-fifth of the total body length). The eyes are relatively large. The dorsal fin is located roughly at the center of the body and stands clearly anteriorly to the small pelvic fins. The pectoral and the anal fins are also remarkably small. The homocercal caudal fin is strongly forked. The fish has distinctive hexagonal scales with a thin ganoid layer. The teeth are small and pointed. Body size: Middle Triassic *Pholidophorus* are no larger than 10 cm. In the Jurassic, fish of this genus reached a maximum length of approximately 30 cm. Systematically, *Pholidophorus* is situated on the transition

Figure 11. | *A:* Pholidophorus. *Collection H. Winkelhorst.* *B:* Pholidophorus. *Collection H. Winkelhorst.*

from the bony ganoids to the modern bony fish, the Teleostei, to which they are also often attributed. The *Pholidophorus* species from the Vossenveld Formation is one of the earliest representatives of this genus and can still, by its physical characteristics, be classified as belonging to the bony ganoids.

Lifestyle: A fast swimming fish with a pelagic way of life. It probably lived in shoals in relatively shallow coastal waters. Food: small fish and crustaceans.

Fossils: In Winterswijk a limited number of fossils of *Pholidophorus* have been found. Some more or less completely preserved specimens (Fig. 11A & 11B) are approximately 7 cm long. Loose solitary scales, easily recognized by their characteristic hexagonal shape, are frequently found.

Sarcopterygii (Lobe finned fishes)

All bony fishes described above belong to the subclass of the ray-finned fishes (Actinopterygii). However, based on several unmistakable fossils, there is also an appealing representative of the subclass of the lobe-finned fishes (Sarcopterygii) known from the Vossenveld Formation.

Coelacanthus
Order: Coelacanthiformes
Family: Coelacanthidae
Genus: *Coelacanthus* sp.

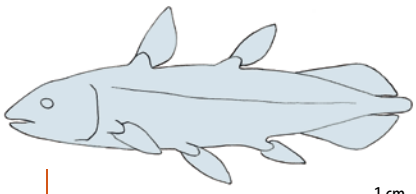

Figure 12. | Coelacanthus.

Characteristics: Medium to large fish with a fairly high, mostly elongated body. The head is rather pointed. Characteristic of the Sarcopterygii are the lobe-shaped fins with a fleshy basis (Fig. 12). The fin rays are greatly ossified. The Coelacanthidae possess two dorsal fins and a very striking, large diphycercal tail (Fig. 12B). The cycloid scales are thin and do not have a ganoid layer. The scales have clear concentric growth rings on the anterior part (the part covered by the preceding and overlying scale) and a structure of small nodules at the back (the visible part of the scales). Size: body length up to approx. 40 cm.

Lifestyle: The Coelacanthidae lived near the bottom, presumably usually in relatively deep water. The behaviour of these remarkable fishes could be studied by observing the living coelacanthiform *Latimeria*. This living coelacanth, of which two species are presently known, was discovered in 1938. It can be considered a 'living fossil'.

Fossils: From the Vossenveld Formation, only a few fossils of (parts of) Coelacanthidae are known (Fig 12A & 12B). The well-recognizable, light brown colored, cycloid scales are found quite often though.

Identification

The generic and specific identification of fish fossils in general and in the Muschelkalk in particular, is in many cases troublesome or rather problematic. This is caused by a number of factors. First of all, remains of fish are generally heavily fragmented as a

result of taphonomic processes (see below). Therefore, most fish fossils only consist of one or just a few elements. Logically, scales are by far the most abundant (loose) finds; these can often be identified by the scale type (see below), but usually not on the genus level, let alone on the species level. This not only because different fish species can possess similar scales, but also because a single fish has a multitude of differently shaped scales, depending on the position of the scales on the body of the fish. In addition, regular ontogenetic changes occur from the juvenile stages to the adult fish in the same species. In fish, this ontogenetic development is often accompanied by clear morphological changes. Also, sexual dimorphism can occur within the same species, in which case there are differences in the (external) characteristics between the two sexes. Most of the fish from the Vossenveld Formation described in this article are identified to their generic name. Many fish fossils lack the necessary details to warrant a scientific designation on the species level. In the meantime, so much material is available that further ichthyological research on the fossils from the Vossenveld Formation should yield more precise identifications, as recent research on *Saurichthys* (Maxwell *et al.*, 2016) and *Eosemionotus* (Wijngaarden *et al.*, 2019) from Winterswijk has shown.

Scales

The most frequent and widespread fossil fish remains in Winterswijk are scales. Scales form in the upper skin layer and are part of the dermal skeleton. So far, two types of scales are found in the Vossenveld Formation.

By far the most abundant are ganoid scales (Fig. 13A). These thick scales usually articulate with a type of peg-and-socket connection and are composed of three layers: a base layer of lamellar bone, a middle layer of dentin and a ganoid (enamel-like) layer on top. This ganoid layer is usually dark brown to glossy black when fossilized. The scales are roof-panting (partly overlapping) on each other. Because of the thickness of the scales, they form a relatively stiff and heavy protective armor, causing fish with such an exoskeleton to be supposedly less mobile. The dimensions, shape and thickness of the ganoid scales vary very strongly.

FIGURE 12AB. | *A:* Coelacanthus *sp. Collection H. Winkelhorst. B:* Coelacanthus *sp. Posterior part, tail to the right, just after discovery in 2014. Private collection.*

Additionally, we occasionally find cycloid scales (Fig. 13B), a flexible type of scale also found in recent Actinopterygii. These have a more or less round shape with concentric 'growth rings'. They are much thinner than the ganoid scales and do not possess a ganoid coating. In Winterswijk they are found fossilized with a light brown color.

Taphonomy

Taphonomy is the science that investigates and describes the decay and fossilization of dead organisms, from the moment an animal dies to the moment it is found. Certain conditions and processes determine whether and how a dead fish fossilizes. In the Muschelkalk Sea near present-day Winterswijk, we find, as mentioned above, varying environmental circumstances. This is reflected in the layering of the Muschelkalk in the quarry. These different circumstances also result in varying conditions for fossilization over time. This is demonstrated by the extent to which fish fossils occur in certain layers and also by the degree of conservation of these fossils.

The following aspects are of (negative) influence on the fossilization process of fish in the Muschelkalk sediments in Winterswijk: feeding by scavengers; bioturbation by the activity of benthic organisms; the influence of waves and currents. Also, the relatively oxygen-rich conditions in the shallow coastal water, compared to some classical 'Konservat Lagerstätten', ensures a quicker dissolution of the fish residues. Additionally, the bodies of most fish in the Anisian do not possess a (fully) ossified (endo)skeleton, a situation that is not favorable to articulated fossilization. However, very well-preserved fish fossils can be found in certain layers. Especially when dead fish were covered relatively quickly by sediment, they were less vulnerable to scavengers and water movements.

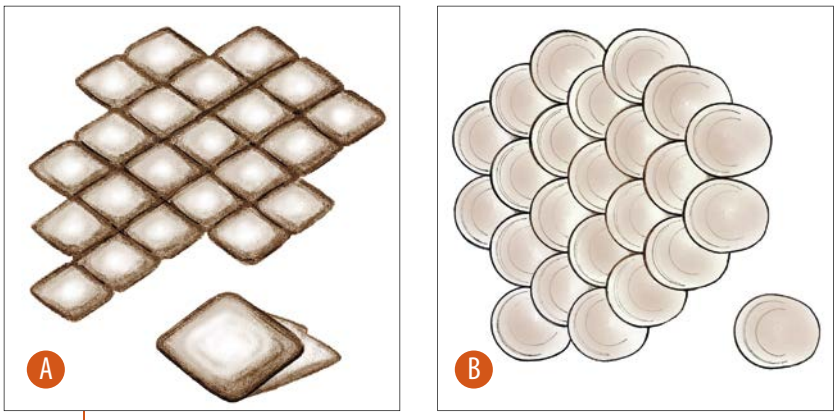

FIGURE 13. | A: *Ganoid scales B: Cycloid scales.*

Due to quick burial, often in a very fine-grained and therefore dense mud layer, the location of the remains may have had a reduced oxygen level, which will have limited predation by benthic animals and infestation by micro-organisms.
The Vossenveld Formation of Winterswijk largely consists of layers of very fine carbonate sediments. Many of these layers contain remnants of fish, but only a few have produced articulated fish remains that are clearly preserved in more favourable conditions for fossilisation. It is mainly in these layers where the most interesting fish fossils may be found for future studies.

Abstract
Over the years, a significant number of fish fossils have been found in the Winterswijk Muschelkalk quarry. Most commonly, loose scales and other unarticulated remains are found. More or less complete fossilized fish are relatively rare. The species richness of the fish fauna in the Vossenveld Formation seems to be quite limited. This is in conjunction with the specific circumstances that determined the local environment and thus the ecosystem in situ. However, since the publication of the noteworthy article on the fish of the Winterswijk Muschelkalk by Oosterink and Poppe (1979), some additional species have been discovered. Here, we provide a complete overview of the species of fish that have been identified to date from the Winterswijk Muschelkalk quarry.

Samenvatting
In de loop der jaren is in de Winterswijkse Muschelkalkgroeve een aanzienlijk aantal visfossielen gevonden. Het meest worden losse schubben en andere ongearticuleerde resten aangetroffen. Relatief zeldzaam zijn min of meer complete fossiele vissen. De soortenrijkdom van de visfauna in de Vossenveld Formatie lijkt vrij beperkt te zijn. Dit hangt samen met de specifieke omstandigheden die het lokale milieu en daarmee het ecosysteem ter plaatse bepaalden. Sinds de publicatie van het nog altijd zeer lezenswaardige artikel over de vissen van de Winterswijkse Muschelkalk van Oosterink en Poppe (1979), zijn er evenwel enkele aanvullende soorten ontdekt. Getracht wordt hier in beknopte vorm een volledig overzicht van de tot nog toe gedetermineerde vissoorten uit de Winterswijkse Muschelkalkgroeve te geven.

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The full list of references can be found at: http://www.geologienederland.nl > Grondboor & Hamer > Staringia 16.
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