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Large *Centrophorus* (Chondrichthyes, Squaliformes) of the Belgian Neogene continental shelf.

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ABSTRACT: A number of isolated teeth of gulper sharks (genus *Centrophorus* Müller & Henle, 1837) have been recovered from Neogene sands in the Antwerp area, marking the first occurrence of the genus *Centrophorus* in the fossil record of Belgium and the North Sea Basin. The precise stratigraphic origin of these teeth could not be established, but the taphonomic condition strongly suggests a Late Miocene or Early Pliocene age, although reworking from older Miocene strata cannot be excluded. These teeth are remarkable for the presence of serrated cutting edges of both upper and lower teeth as well as their large size. The teeth, that measure up to 1 cm, are the largest fossil *Centrophorus* reported in literature. The subtle differences between the teeth of different *Centrophorus* species and the paucity of comparative extant material prohibit specific attribution, but the teeth pertain to individuals that equalled the largest extant species. The occurrence of these large *Centrophorus* in the Belgian deposits is remarkable as *Centrophorus* usually prefers deeper waters.

KEYWORDS: Centrophoridae, Pliocene, Kattendijk Formation, Deurganckdok, Belgium, North Sea Basin.

1. Introduction

Neogene selachian remains are very common in the Antwerp area and have been studied for more than 150 years (*e.g.* Le Hon, 1871; Leriche, 1926, 1951; Herman et al., 1974; Herman, 1979; De Ceuster, 1987; Bosselaers et al., 2004; Reinecke & Hoedemakers, 2006; De Schutter, 2009, 2011). Antwerp, situated at the south-western margin of the North Sea Basin (Fig. 1), is rich in sediments that were deposited in shallow marine environments (Laga et al., 2001). This is supported by the shark faunas presenting mostly species of shallow seas. Squaliform sharks, that comprise the majority of extant deep-water genera (Compagno, 1984), are consequently represented by only a few genera. *Squalus* Linnaeus, 1758 and *Isistius* Gill, 1865 were reported from the Belgian Miocene (De Ceuster, 1987; pers. data), while *Squalus*, *Somniosus* Lesueur, 1818 and *Oxynotus* Rafinesque, 1810 have been reported from Pliocene deposits (Herman et al., 1974). Except for *Isistius*, these genera are still present in the modern North Sea (George, 2009). Although commonly associated with the margins of the continental shelf, squaloids may occur in shallow waters: *Squalus acanthias* Linnaeus, 1758 is often found in enclosed bays and estuaries, and can even tolerate brackish water (Compagno, 1984). *Somniosus microcephalus* (Bloch & Schneider, 1801) may occur at the surface in shallow bays and river deltas during colder months, retreating into deeper water when temperature rises (Bigelow & Schroeder, 1948) and *Centrophorus squamosus* (Bonnaterre, 1788) occasionally ventures onto continental shelves up to the surface (Compagno, 1984).

The aim of this paper is to report on the first occurrence of *Centrophorus* in the fossil record of Belgium and the North Sea Basin. In addition, these teeth merit attention for their remarkable morphology: the Antwerp specimens are distinctly characterised by their size and serrated cutting edges. Their presence is remarkable as the presence of fossil *Centrophorus* is usually associated with deep-water deposits (*e.g.* Ledoux, 1972; Adnet, 2006).

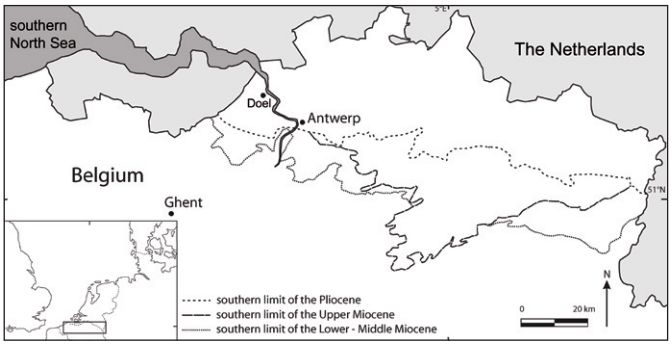

Figure 1. Location of the study area near Antwerp in northern Belgium, showing the southern margin of the North Sea Basin during the Neogene. Inset: southern North Sea. (Map courtesy by S. Louwye)

2. Locality and stratigraphy

Miocene and Pliocene deposits are restricted to the northern part of Belgium and were deposited in a shallow marine environment along the south-western margin of the North Sea Basin (Fig. 1) (Laga et al., 2001; De Schepper et al., 2004).

In the Antwerp area (Fig. 1), the Miocene is represented by the early Burdigalian to Serravallian Berchem Formation (De Meuter & Laga, 1976; Laga et al., 2001; Louwye & Laga, 2007) and the Tortonian Diest Formation (Deurne Sands member) (Louwye, 2002). The Kattendijk Formation was introduced by de Heinzelin (1955) as the lowermost part of the Pliocene. A type locality is only vaguely defined (surroundings of the Kattendijkdok, Amerikadok and Lefèbvredok). Type section is the outcrop of the Verbindingsdok (see De Meuter & Laga, 1976: 137). Vandenberghe et al. (1998) and Louwye et al. (2004) dated it as early Zanclean. The deposition depth of the Kattendijk Formation is estimated at 45-70 m based on bivalves (Marquet, 2004) and 30-50 m based on fish otoliths (Gaemers, 1988), diminishing in successive deposits. Based on dinoflagellate cyst stratigraphy, the age of the Kattendijk Formation is about 5.0 Ma and 4.7-4.4 Ma (Louwye et al., 2004). This formation consists mainly of glauconitic sands, scattered or concentrated shells, with a gravel at its base (De Meuter & Laga, 1976).

In the Antwerp area, *Centrophorus* teeth are occasionally found, but are often confused with teeth of *Somniosus* (pers. obs.). Most *Centrophorus* teeth were collected around the village of Doel, Antwerp harbour, left bank of the river Scheldt, East-Flanders province, Belgium (Fig. 1). The Scheldt River is the only maritime access to the port of Antwerp and a minimum depth is guaranteed for ships bound for the Antwerp harbour. As there is a constant process of sedimentation, continuous maintenance and capital dredging is required. The extracted sands are either used in nearby construction sites, or deposited in adjacent areas. Incidentally, the continuous expansion of the harbour provides (temporary) outcrops allowing sampling of the Kattendijk Formation and its basal gravel. The progressive enlargement of the recently dug harbour dock (the Deurganckdok, 2001-2005) provided a unique opportunity to observe and sample *in situ* the basal gravel of the Kattendijk Formation (Herman & Marquet, 2007). Here, the gravel is placed on top of the Miocene Berchem Formation (early Burdigalian) or immediately on the abraded top of the Oligocene Boom Formation (without interbedded Miocene). The faunal assemblages and taphonomic condition in both situations are very different (Herman & Marquet, 2007). Shark remains found in the gravels on top of the Oligocene Boom Clay are usually much abraded and often unidentifiable, whereas those found on top of Miocene sands are much better preserved. It wasn't recorded whether the *in situ* specimen (TL01, Plate 2A-C) was found in the gravel on top of the Oligocene clay or Miocene sands, but its preservation strongly suggests the last. *Centrophorus* teeth are strongly labio-lingually compressed and therefore rather fragile. Since the taphonomic condition of all recovered *Centrophorus* teeth is mainly good to excellent, we infer a Late Miocene or Early Pliocene age for these specimens.

3. Materials and methods

Fossiliferous sand was dry sieved at a 10 mm mesh width removing larger fossils and stones. The remaining residues were washed and sieved at 5 and 1 mm mesh width respectively. The content of the 5 mm sieve was examined on-site. Finer residue (<5 mm) was processed off-site.

One specimen (TL01, Plate 2A-C) was found in the *in situ* basal gravel of the Kattendijk Formation (Deurganckdok); all other teeth (DS01-04, LK01-02) in displaced and mixed sediments originating from the Deurganckdok or similar construction sites in the same large area.

14 extant *Centrophorus* jaws of sharks measuring between 43 and 130 cm total length (TL), were examined for comparison (Dirk & Maria Hovestadt Collection, see Figure 3).

Systematics follows Compagno (2005) and descriptive terminology is according Cappetta (1987).

4. Systematic palaeontology

Class CHONDRICHTHYES
Order SQUALIFORMES
Family CENTROPHORIDAE
Genus CENTROPHORUS Müller & Henle, 1837
Type Species: *Squalus granulosus* Bloch & Schneider, 1801
Species: *Centrophorus* sp.
(Plates 1-3)

***Dimensions*:** Height and width of the figured specimens are shown in Table 1 (see Fig. 2).

***Description*:** These teeth are labio-lingually compressed, showing the basal face of the root in lingual aspect. Lower teeth (DS01-04, Plate 1A-H; LK02, Plate 2G-H) are higher than they are wide and have a broad cusp. The principal cusp is directed distally. A distinct convex distal blade is present, separated from the principal cusp by a notch. Both blade and cusp are finely serrated.

The lingual face of specimen DS01 (Plate 1A) shows a distinct small uvula which reaches the lingual bulge of the root (the ridge running mesio-distal over the lingual root face). Probably due to abrasion, the uvula is absent in the teeth DS02 (Plate 1C), DS03 (Plate 1E) and DS04 (Plate 1G). The uvula points downwards to a large central foramen that is well developed, just below the lingual bulge of the root. Several smaller foramina are generally situated mesially and/or distally from the uvula (*e.g.* DS02, Plate 1C). Before recurving downward in a sigmoid curve, the mesial root margin slightly extends mesial beyond the crown at the lingual bulge. The irregularly shaped distal root margin joins the base from the bulge downward in an irregularly shaped blunt curve. Base and mesial margin join in a sharp curve and the root is constricted just below the bulge, which is more developed mesially. As result of tooth interlocking a distal depression is present between blade and bulge.

In labial aspect, an apron is the most distinctive feature, forming a narrow extension of the crown that reaches almost to the basal margin of the root. Due to abrasion, the apron is poorly visible on some specimens. If the apron is preserved, its mesial and distal margins run either parallel (*e.g.* DS01, Plate 1B), or gradually converge towards the end (*e.g.* DS02, Plate 1D). Mesial from the apron, below the crown base, one distinct lateral foramen is often present (*e.g.* DS04, Plate 1H). The crown base joins the apron mesially and distally in a sharp curve of which the distal curve is sometimes very irregularly shaped, accentuating several lateral foramina just below the crown margin (*e.g.* DS02, Plate 1D).

One tooth (DS01, Plate 1A-B) has the mesial cutting edge in a more pronounced sigmoid shape with the distal cutting edge concave rather than straight or convex.

Two upper teeth were recovered, one of an anterior (LK01, Plate 2D-F) and one of a more lateral position (TL01, Plate 2A-C). Both have an upwardly directed cusp. LK01 lacks a distal blade and both cutting edges are concave and finely serrated (Plate 2F). The tooth is higher than wide, with an almost square root. The lingual face presents a poorly developed uvula and the bulge is situated close to the basal margin of the crown. A large prominent infundibulum is located just below the bulge. At the labial face, the apron is replaced by long, irregularly shaped worn extensions with various small foramina in-between.

TL01, which represents a more lateral position, has a concave mesial- and convex distal cutting edge. The crown and distal blade are finely serrated (Plate 2C). The tooth is slightly higher than wide. Lingually a pronounced infundibulum is present, dividing the bulge. Most of the crown's enamel has worn off. On the labial side, the outline of the apron is distinctly visible. It slightly narrows while extending to near the basal margin of the root. A small foramen divides the lowest part of the apron. Some foramina are present mesially and distally from the apron, just below the crown base.

5. Discussion

The Centrophoridae (Chondrichthyes: Squaliformes) comprise two genera, *Centrophorus* and *Deania* (Compagno, 2005). Generic attribution of teeth is straightforward based on the median foramina on the lingual face of the root. In *Deania* there are two foramina present, whereas in *Centrophorus* these two are fused into a so called infundibulum (Ledoux, 1970). All described teeth show the presence of a single foramen, warranting their assignment to *Centrophorus*. The genus *Centrophorus*, proposed by Müller & Henle, 1837, has had a very complex taxonomic history due to a poor original description of most species, significant intraspecific morphological variation and ontogenetic changes in dermal denticle and tooth morphologies associated with growth and sexual dimorphism (White et al., 2008). Since there are only very subtle differences between the teeth of different *Centrophorus* species (Ledoux, 1970; Adnet, 2006; Cigala-Fulgosi et al., 2009), the teeth described in the present study are kept in open nomenclature.

The female dentition is characteristic by teeth pointing more strongly distally than in males which show a more upright pose (Garrick, 1959; Ledoux, 1970). The tooth described as having a more sigmoid mesial and concave distal cutting edge (DS01, Plate 1A-B)

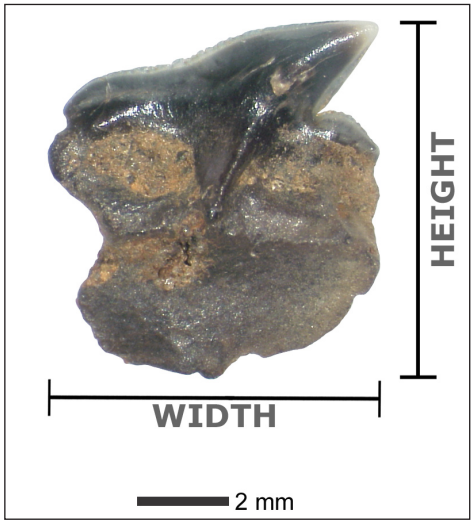

Figure 2. Measurements

Specimen	Figure	Height	Width
DS01	Plate 1, figs A-B	7.8	6.9
	Plate 3, figs A-B		
DS02	Plate 1, figs C-D	10.5	7.7
	Plate 3, figs C-D		
DS03	Plate 1, figs E-F	10.0	8.3
	Plate 3, figs E-F		
DS04	Plate 1, figs G-H	10.3	8.1
	Plate 3, figs G-H		
TL01	Plate 2, figs A-C	5.7	4.8
	Plate 3, figs I-J		
LK01	Plate 2, figs D-F	6.9	3.4
	Plate 3, figs K-L		
LK02	Plate 2, figs G-H	8.0	6.9
	Plate 3, figs M-N		

Table 1. Measurements (mm)

likely belonged to a female individual, indicating that both sexes were present in the Antwerp area.

The genus *Centrophorus* consists of at least 12 species (Compagno, 2005; White et al., 2008): *Centrophorus granulosus* (Bloch & Schneider, 1801), *C. squamosus* (Bonnaterre, 1788), *C. harrissoni* McCulloch, 1915, *C. moluccensis* Bleeker, 1860, *C. atromarginatus* Garman, 1913, *C. niaukang* Teng, 1959, *C. acus* Garman, 1906, *C. isodon* (Chu, Meng & Liu, 1981), *C. lusitanicus* Bocage & Capello, 1864, *C. tessellatus* Garman, 1906, *C. westraliensis* White et al., 2008 and *C. zeehaani* White et al., 2008. *C. granulosus*, *C. lusitanicus, C. niaukang* and *C. squamosus* occur in the NE Atlantic (Compagno et al., 2005; Iglésias, 2011). Only *C. squamosus* seems to be present in the North Sea (George, 2009).

Centrophorus has an extensive and worldwide fossil record. The Centrophoridae lineage goes back until the Turonian (Adnet & Cappetta, 2001) or possibly even the Cenomanian (Adnet et al., 2008). In Europe the genus was reported from Tertiary deposits of France *(e.g.* Cappetta et al., 1967; Ledoux, 1972; Cappetta, 1975; Cappetta & Nolf, 1991; Adnet, 2006), Czech Republic (*e.g.* Brzobohaty & Kalabis, 1970), Germany *(e.g.* Probst, 1879; Barthelt et al., 1991), Slovakia (*e.g.* Holec et al., 1995), Hungary (*e.g.* Kocsis, 2007), Spain (*e.g.* Mañé et al., 1996), Italy (*e.g.* Landini, 1977; Cappetta & Cavallo, 2006; Marsili, 2007; Marsili & Tabanelli, 2007) and Switzerland (*e.g.* Fischli, 1930).

Serrations are present in several squaliform genera. In *Squalus* (see Cappetta, 1987; Herman et al.,1989), *Somniosus* (see van der Brugghen, 1992) and *Centrophorus* (see Bigelow & Schroeder, 1957; Ledoux, 1970), the development of serrations is linked to ontogenetic development: juveniles have a smooth cutting edge and serrations develop gradually toward the adult stage (Ledoux, 1970; Herman et al.,1989; van der Brugghen, 1992; Adnet, 2006). Serrations on the lower teeth are a very variable feature in *Centrophorus* (Compagno, 1984) and seem to occur in various species. Serrations were reported in extant *Centrophorus granulosus* (see Herman et al., 1989), *C. squamosus* (see Ledoux, 1970), *C. tessellatus, C. atromarginatus* and *C. acus* (see Bigelow & Schroeder, 1957), *C. moluccensis* (see Bass et al. 1976), *C. harrissoni* and *C. niaukang* (see Compagno, 1984). Likewise, the fossil record regularly yields serrated *Centrophorus* teeth: Cappetta & Nolf, 1991; Cappetta & Cavallo, 2006; Adnet, 2006; Marsili & Tabanelli, 2007; Marsili, 2007. These serrations are mostly fine and limited to the mesial cutting edge of lower teeth. However, fine serrations on upper teeth were reported on larger, extant *C. granulosus* by Ledoux (1970: 330), on extant *C. squamosus* by Garrick (1959), and by Adnet (2006) describing Eocene specimens of France. Bocage & Capello (1866: 26), describing extant *C. granulosus*, only mentioned serrations on lower teeth in the text, but nevertheless figured a serrated upper tooth as well (Pl. 1, fig. 3e). Long (1992), describing Eocene *Centrophorus* teeth from the Antarctic Peninsula, figured lower teeth with fine to coarse serrations on the mesial and distal cutting edges. An upper tooth referred to *Deania* in the same study (Fig. 6A-B) was later referred to *Centrophorus* by Adnet (2006: 25). This specimen appears to possess some fine serrations, despite being described as smooth by Long (1992: 18). The size of these teeth, inferred from the figures, is about 5 mm for lower (Long, 1992: fig. 6E) and 3.8 mm for upper teeth (Long, 1992: fig. 6A). With the exception of their larger size, the Belgian teeth are very similar to the Antarctic specimens. Due to the absence of smaller fossil *Centrophorus* teeth from the same deposits and larger extant comparable specimens being unavailable to the authors (*e.g.* teeth of *C. niaukang*), specific attribution can not be done. However, since the development of serrations is so obviously linked to ontogeny in *Centrophorus*, and (fine) serrations are common in *Centrophorus* species, the occurrence of coarse serrations on very large specimens of any *Centrophorus* might be expected. Therefore it seems likely that the teeth described here represent a large form of a known species.

Centrophorus teeth are uncommon in the Antwerp deposits, as are teeth of the other squaloid sharks like *Isistius, Somniosus* and *Oxynotus*. This could either mean that these species were occasional visitors to the area, or that their standing stocks were simply low. The absence of teeth of smaller individuals could be the result of the collecting method (mesh width), especially since most teeth originate from the lower jaw of adult sharks (largest possible teeth). However, since collectors frequently recover small teeth of other species, we favour another hypothesis: the occurrence of these large *Centrophorus* specimens in the shallow Antwerp waters may simply reflect a habitat preference for these large adults. Such a hypothesis would be consistent with the absence of smaller teeth of this species in these Belgian deposits. *Centrophorus* is commonly found along the outer continental shelves and upper slopes, sustaining at 4000 m depth, but usually bottom dwelling at depths between 200 and 800 m (Compagno et al., 2005). Segregation by size, sex and development stage is often recorded among deep-water squaloid sharks (*e.g.* Muñoz-Chápuli, 1984; Yano & Tanaka, 1988), including *Centrophorus squamosus*: Girard & du Buit (1999: 929) demonstrated the existence of an important bathymetrical and geographical segregation; juveniles and pregnant females prefer deeper water than adults. Similar observations were made for *Centrophorus* cf. *uyato* (McLaughlin & Morrissey, 2005).

The largest tooth in the largest examined extant *C. granulosus* (M&D83Z0171, TL = 102 cm) measured 4.6 mm in height against 6.5 mm for the largest *C. squamosus* (M&D81W0165, TL = 130 cm) (Figure 3). The Antwerp specimens, up to 10.5 mm in height (Table 1), represent the largest fossil *Centrophorus* teeth ever reported and appear larger than the teeth of most extant species, with the possible exception of *C. niaukang* Teng, 1959. This largest extant species attains a TL of at least 170 cm (Compagno et al., 2005; Iglésias, 2011). We could not find information about the size of its teeth in the literature available to us, but it can be hypothesized that the teeth of *C. niaukang* attain or perhaps even exceed the size of the fossil teeth in the present study.

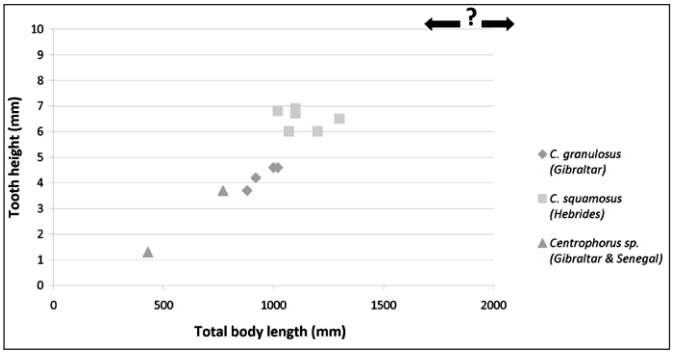

Figure 3. Relation between tooth height (vertical) and total body length (horizontal) in extant *Centrophorus*. The question mark indicates the size of the largest fossil teeth, with arrows indicating a possible size range.

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Plate 1. *Centrophorus* sp.
Scanning electron microscope (SEM) images.
Scale bar = 2 mm

DS01 (A-B) - lower tooth - De Schutter collection, *ex situ*, "Indaver" (H-1940), Doel.
Lingual (A) and labial (B) views.

DS02 (C-D) - lower tooth - De Schutter collection, *ex situ*, "Indaver" (H-1940), Doel.
Lingual (C) and labial (D) views.

DS03 (E-F) - lower tooth - De Schutter collection, *ex situ*, Churchilldok, Hoevenen.
Lingual (E) and labial (F) views.

DS04 (G-H) - lower tooth - De Schutter collection, *ex situ*, Deurganckdok, Doel.
Lingual (G) and labial (H) views.

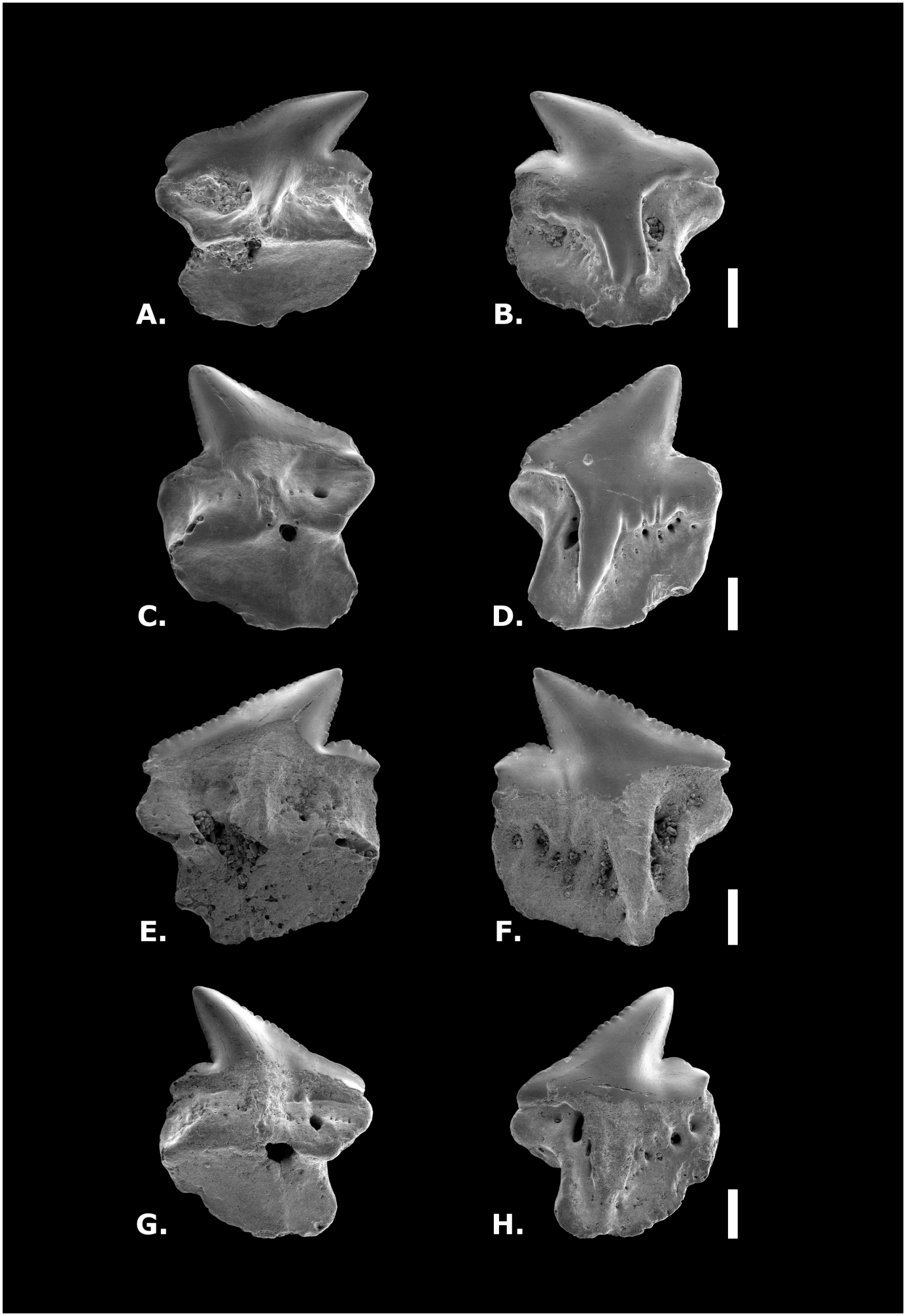
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Plate 2. *Centrophorus* sp.
Scanning electron microscope (SEM) images.
Scale bar = 2 mm

TL01 (A-C) - upper tooth - Theo Lambrechts collection, ***in situ***, Deurganckdok, Doel.
Lingual (A) and labial (B) views. Detail of serrated mesial cutting edge (C).

LK01 (D-F) - upper tooth - Lex Kattenwinkel collection, *ex situ*, Churchilldok, Hoevenen.
Lingual (D) and labial (E) views.
Detail of serrated mesial and distal cutting edge (F).

LK02 (G-H) - lower tooth - Lex Kattenwinkel collection, *ex situ*, "Indaver" (H-1940), Doel.
Lingual (G) and labial (H) views.

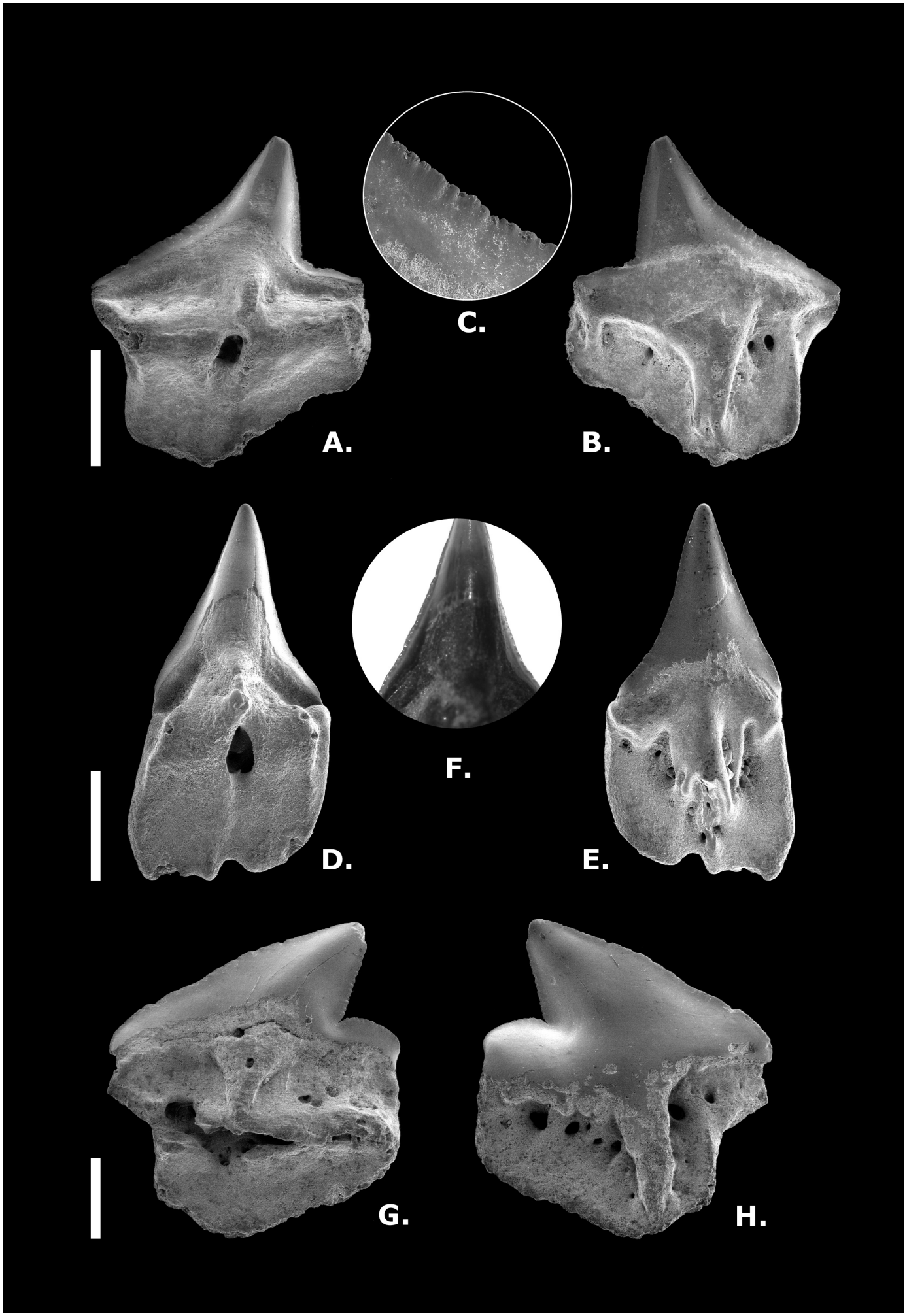
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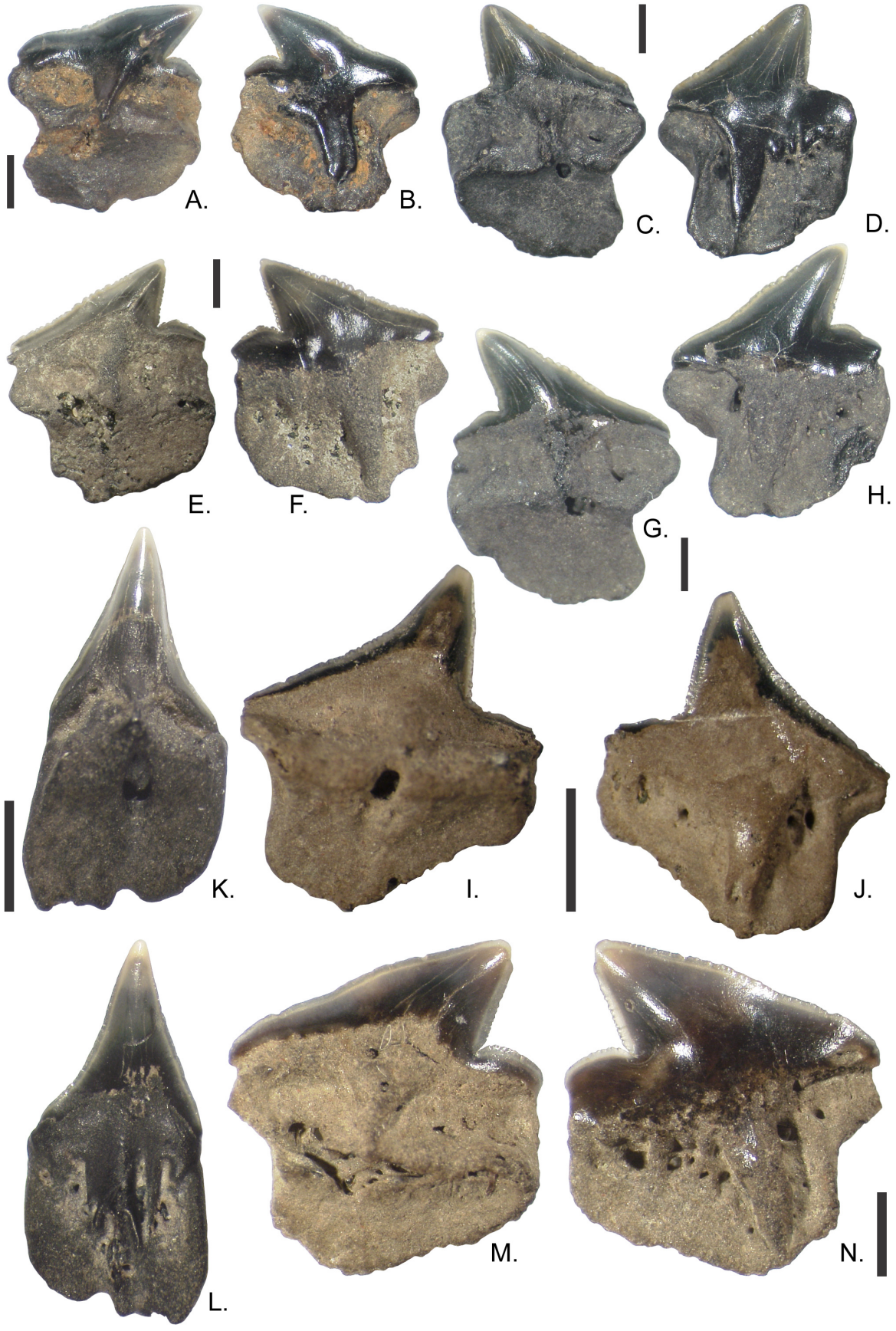
Plate 3. *Centrophorus* sp.
Scale bar = 2 mm

DS01 (A-B) - Lingual (A) and labial (B) views.
DS02 (C-D) - Lingual (C) and labial (D) views.
DS03 (E-F) - Lingual (E) and labial (F) views.
DS04 (G-H) - Lingual (G) and labial (H) views.

TL01 (I-J) - Lingual (I) and labial (J) views.
LK01 (K-L) - Lingual (K) and labial (L) views.
LK02 (M-N) - Lingual (M) and labial (N) views.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