Swiss J Geosci (2016) 109:1–16
DOI 10.1007/s00015-015-0194-z

Taphonomic analysis of *Saurichthys* from two stratigraphic horizons in the Middle Triassic of Monte San Giorgio, Switzerland

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Received: 17 November 2014 / Accepted: 26 July 2015 / Published online: 30 December 2015

Abstract Excavations of Middle Triassic strata at Monte San Giorgio (Switzerland–Italy) have famously recovered a range of reptiles whose affinities, morphology and preservation have been extensively described. The locality has also yielded a contemporaneous and equally diverse fish fauna that has yet to be described to the same degree. To address this imbalance, a taphonomic study was undertaken using the actinopterygian *Saurichthys*, a relatively abundant taxon found in the Besano Formation (latest Anisian–earliest Ladinian) and Cassina Beds of the Meride Formation (early Ladinian). Specimens from each horizon were scored for articulation and completeness across ten anatomical units, the resulting datasets being used to determine a taphonomic model and investigate preservational variation through time. *Saurichthys* showing moderate to high articulation and high completeness occur in both horizons but states of low articulation and moderate completeness are only present in the Besano Formation. The same feature is apparent in corresponding unit plots, suggesting different environmental conditions were present during deposition of each horizon, specifically those that reduced articulation and completeness during a prolonged residence on the sediment surface.

Editorial handling: D. Marty.

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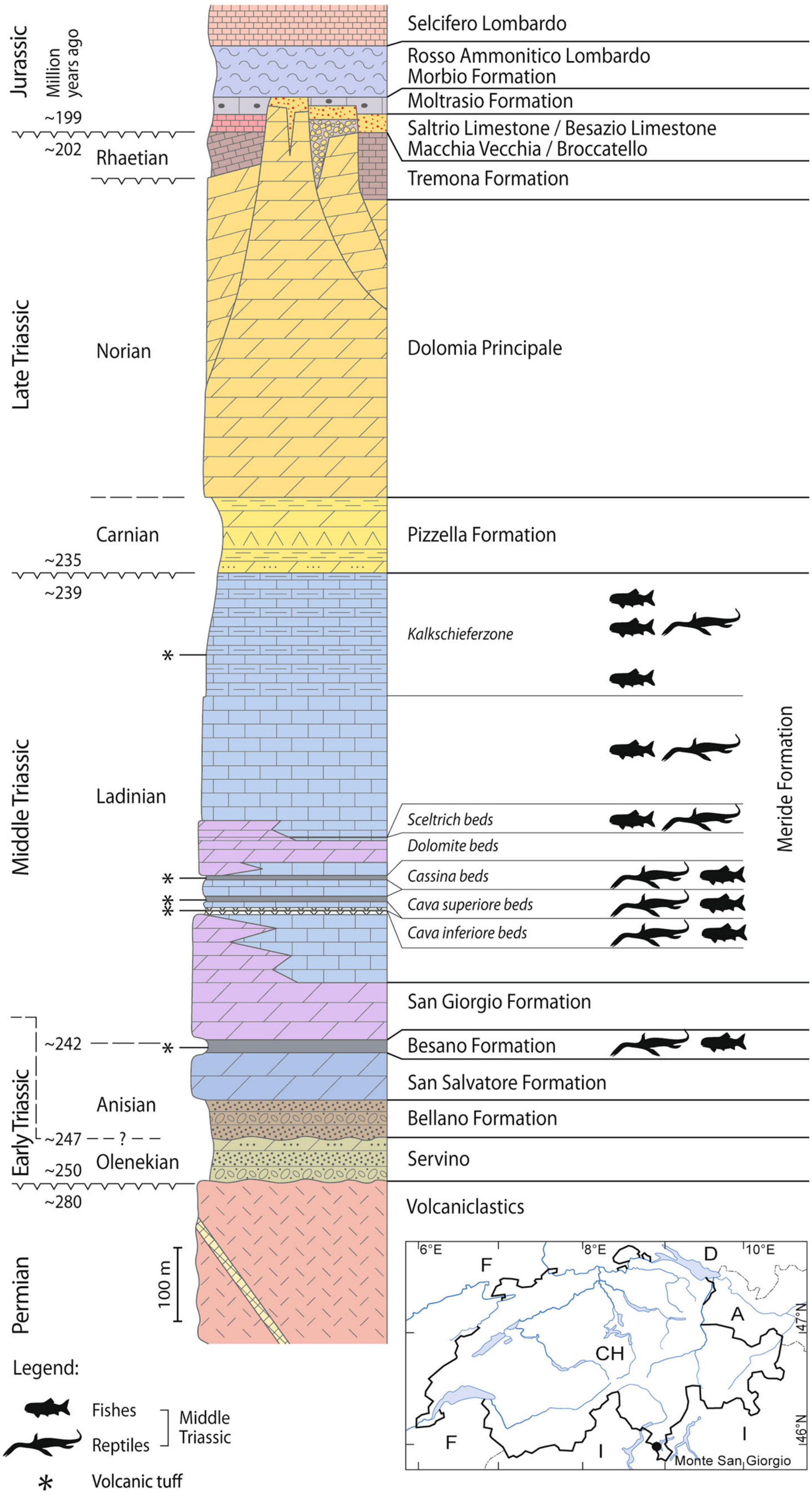
Keywords *Saurichthys* · Actinopterygii · Skeletal taphonomy · Palaeoenvironment

1 Introduction

The excellent preservation, diversity and relative abundance of the fossilised biota from Monte San Giorgio (MSG) on the Switzerland–Italy border has led to its recognition as a UNESCO world heritage site in 2003 and 2010 that today is still a source of Middle Triassic vertebrates, invertebrates and plants (Fig. 1). These originate from five horizons, primarily the Besano Formation (latest Anisian–earliest Ladinian), but also the Cava Inferiore, Cava Superiore and Cassina Beds of the Meride Formation (early Ladinian), and the Kalkschieferzone (late Ladinian), deposited in an intra-platform basin on a shallow carbonate shelf at the north-western rim of the deeper Tethys Ocean at about 20 degrees north latitude (Bernasconi 1991; Röhl et al. 2001; Furrer 1995, 1999, 2003; Furrer and Vandelli 2014). Water depth is estimated to have been 30–130 m with the water column stratified into well oxygenated surface waters and predominantly but not continuously anoxic bottom conditions. The site is most famous for the skeletal remains of aquatic and terrestrial reptile fossils, representing the Nothosauridae, Pachypleurosauridae, Placodontia, Ichthyosauria, Protorosauria, Thalattosauria and Rauisuchia. The morphology of the majority has been described in detail, notably by Peyer (1931a, b, 1932, 1936a, b, 1937), Zangerl (1935), Kuhn-Schnyder (1964, 1974), Krebs (1965), Wild (1974), Rieppel (1989), Sander (1989) and Nosotti and Teruzzi (2008). Their taphonomy has also been investigated, highlighting a number of key preservational features and conditions in the depositional environment

Fig. 1 Stratigraphic section and geographical location of the Monte San Giorgio locality on the Switzerland–Italy border. The sources of reptile and fish fossils are also indicated



(Wild 1974; Sander 1989; Furrer 1995, 2003; Furrer and Vandelli 2014; Beardmore 2012; Beardmore et al. 2012).

Less well-known is the even more diverse array of fossilised fish (see overviews in Bürgin 1999; Furrer 2003; Etter 2002). To date, over 30 genera have been recorded from almost all major groups, such as Chondrichthyes, Actinistia, basal Actinopterygii and Neopterygii (Kuhn-Schnyder 1964; Schwarz 1970; Rieppel 1980, 1981, 1985, 1992; Bürgin et al. 1989; Bürgin 1990, 1992, 1996, 1999, 2004; Tintori 1992; Furrer 1995, 2003; Mutter 1998, 2004; Tintori and Lombardo 1999; Romano and Brinkmann 2009; Stockar 2010; Brinkmann and De Baets 2012; Lombardo et al. 2012). In contrast to the reptiles, studies of the fish are often very general. For example, Tintori's (1992) description of preservation of the Besano Formation fish biota was undertaken as a whole and as one of several fish-bearing, black shales from the Middle–Upper Triassic of the Southern and Eastern Alps of Europe. Furthermore, the focus of this particular study was the degree of oxygenation in the bottom waters of respective depositional basins. Stockar's (2010) report of fish preservation, although focused on specimens from the Cassina Beds, is also not specific to any particular vertebrate group.

A good number of very specific morphological studies regard the actinopterygian *Saurichthys*. Rieppel (1985, 1992) and Maxwell et al. (2015) provided a detailed description of the taxon, which is represented at MSG by six species: *S. curionii*, *S. macrocephalus*, *S. costasquamosus*, *S. paucitrichus*, *S. breviabdominalis*, *S. rieppeli*. Characters distinguishing these are noted as overall size, fin structure, skull proportions and features of the dentition (see Rieppel 1992; Maxwell et al. 2015). Investigations of the distribution of *Saurichthys* species through time has found that *S. costasquamosus*, *S. paucitrichus, S. breviabdominalis* and *S. rieppeli* occur in the Besano Formation with *S. curionii* and *S. macrocephalus* occurring in the succeeding Cassina Beds (Rieppel 1992; Maxwell et al. 2015). Reproductive strategies have also been discussed (Rieppel 1985; Bürgin 1990). With regard to taphonomy, Stockar (2010) provides comments on the preservation of *Saurichthys*, as the dominant fish taxon from the Cassina Beds. Renesto and Stockar (2009) described three examples of presumably adult *Saurichthys* from the Cassina Beds with embryonic skeletons, many of which show dark eye patches, preserved in the abdominal region of each. Excellent preservation of a further specimen of *Saurichthys* from the Cassina Beds has allowed the interrelationship of skeletal elements and soft tissue to be observed (Maxwell et al. 2013).

The above knowledge of *Saurichthys*, combined with a relatively high abundance of fossil specimens at MSG, makes it an ideal subject for a comprehensive preservational study of a fish taxon. This was undertaken with the primary aim of determining a general taphonomic model that could, secondarily, be tested against various parameters relating to the surrounding environment and morphology. For example, the occurrence of specimens in more than one fossiliferous horizon at the MSG locality, and in most cases from known beds, offers the opportunity for variation in preservation through time to be tested and the potential causes of any variation to be inferred. *Saurichthys* are also found in black shale and carbonate (dolomite and limestone) lithologies, allowing facies variation to be tested. In addition, although normally less than a metre long, the total body length of *Saurichthys* varies from a few centimetres to several decimetres depending on species and ontogenetic stage, which might also influence preservation (Rieppel 1992).

2 Method

Taphonomic methodologies accommodating the morphology of fish are not abundant or evident in literature. The analysis herein was undertaken using a modified version of a methodology described by Beardmore (2012) and Beardmore et al. (2012), used to investigate preservation of Middle Triassic reptiles from MSG possessing a typical tetrapod ('*Serpianosaurus*-type') body plan. In accordance with these studies, the skeleton of *Saurichthys* was divided into a series of anatomical units, each scored for articulation and completeness. In contrast to the original study on pachypleurosaurids, in which the anatomical divisions were the head, neck, dorsal vertebrae, tail, ribs and four limb units, the *Saurichthys* were divided into a head, axial skeleton (in which only the haemal and neural arches are present), caudal fin, scale row (up to six lines), left and right pectoral fin, left and right pelvic fin, dorsal fin and anal fin units to accommodate and utilise the main features of the piscean morphology: the 'fish-type' body plan [Fig. 2; see Rieppel (1992, table 1) for specific *Saurichthys* anatomical details]. In doing so, the number of units was increased from 9 to 10. In addition, the scoring system was modified so that the head and axial skeletal units were scored between 0 and 5, the scale rows 0 to 6, the caudal fin 0 to 4, the left and right pelvic fin 0 to 2, and the left and right pectoral, dorsal and anal fins 0 to 3, amounting to a maximum score of 36. Units that could not be scored because they were either missing from the edge of a slab or obscured by other parts of the skeleton were noted with an 'X' and the possible maximum score was reduced by the score for that particular unit (see Beardmore 2012; Beardmore et al. 2012).

The dataset of scores was used to produce a scatter plot of overall articulation versus completeness values for each specimen ('percentage plots') and scores of articulation

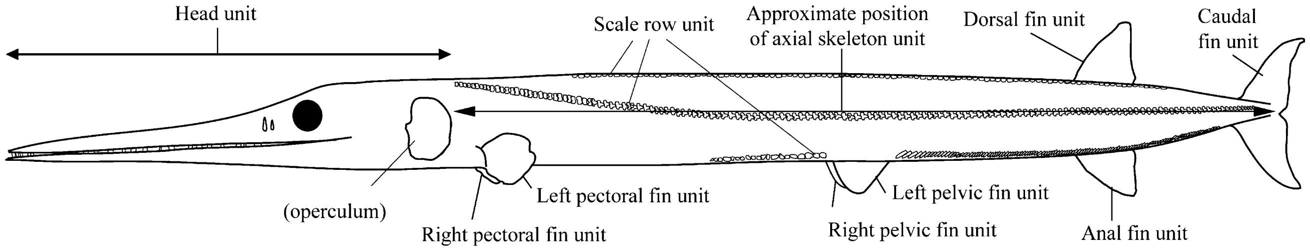


Fig. 2 The basic body plan of the *Saurichthys* skeleton. Anatomical divisions used in the taphonomic analysis are shown with the exception of the axial skeleton unit, which runs approximately mid-line along the length of the body

and completeness for each unit were plotted on a bivariate bubble plot to identify variation within, and between, each anatomical region ('unit plots') (Beardmore 2012; Beardmore et al. 2012). Linear regression lines forced to pass through the 'taphonomic origin', that is, the position of a carcass on a percentage or unit plot in its fully articulated and complete state prior to post-mortem degradation, were fitted to the data in the percentage and unit plots to determine a T value, herein used as a measure of articulation and completeness, or loss thereof. The T value also defines three trends in the distribution of data that are used to interpret the taphonomic pathway of a carcass in the time between death and final burial under sediment (the 'death–burial interval'). As the maximum score in the modified methodology herein varies across the ten anatomical units, the boundaries for trends, as originally described by Beardmore (2012), were also re-defined. Visually, Trend 1 is a horizontal distribution of data (the region of variable articulation–high completeness); Trend 2 is a diagonal distribution (from maximum values of articulation and completeness to the minimum); Trend 3 is a distribution between Trends 1 and 2. Actual values are more difficult to apply, but are determined in the strictest sense by dividing the maximum score for a particular unit into thirds, the uppermost being Trend 1, the lowermost Trend 2, and that between Trend 3. An exception is made herein for the pelvic fin units, which have a maximum score of 2 allowing only 2 trends (Trend 1 and Trend 2) to be defined; these fall between 1 to 2 and 0 to 1, respectively.

The data is further described using Pearson's r^2, reported by Excel and used to express, parametrically, the goodness of fit of the regression line forced to pass through the taphonomic origin, and the Spearman rank-order correlation coefficient (rs) calculated in PAST (PAlaeontological STatistics program; Hammer and Harper 2001) used as a non-parametric measure of the strength of correlation between articulation and completeness. Values for r^2, rs and T are shown below, or within, the plot they relate to. Verbally, the r^2 and rs values are described as low when below 0.35, moderate between 0.35 and 0.65, and high above 0.65 (Beardmore 2012; Beardmore et al. 2012).

3 Materials

All of the MSG *Saurichthys* included herein are housed in the Paläontologisches Institut und Museum der Universität Zürich, Switzerland (PIMUZ), and were collected during the bed by bed excavations under direction of Bernhard Peyer and Emil Kuhn-Schnyder between 1924 and 1975. Preservation is in black shale or laminated carbonate muds, the latter calcitic in the Cassina Beds, but dolomitised in the Besano Formation (Bernasconi 1991; Furrer 1995; Röhl et al. 2001). For the main analysis, *Saurichthys* specimens were included if they comprised more than ten individual elements, had at least two units that could be scored for completeness (but not necessarily articulation) with values of 1 or more on the scale devised, and the scoring of at least 7 of the 10 units was possible, even if the score was 0, as opposed to an 'X' (see above). The resulting dataset comprised 133 'complete' *Saurichthys*, divided into 83 specimens from the Besano Formation and 50 from the Cassina Beds analysed separately to determine models of preservation for each horizon and any variation between. These datasets were also used to investigate the effect of size on preservation. A second dataset of 362 *Saurichthys* was compiled for an investigation of fossil distribution and preservational variation through time. For this investigation, the criterion specified only origination of a specimen from the bed by bed excavations at "P. 902/Mirigioli" (Besano Formation) and knowledge of the source bed (Kuhn-Schnyder 1974; Röhl et al. 2001; Furrer 2003); the majority of specimens were therefore 'fragmentary'.

4 Results

4.1 Overall preservation

The percentage plot for *Saurichthys* (n = 133) shows a distribution of data from moderate to high articulation and high completeness, to poorly articulated and moderately complete (Fig. 3a). Data is sparse in the latter region and entirely absent in the regions of high articulation and completeness, poorly articulated and fully complete, and

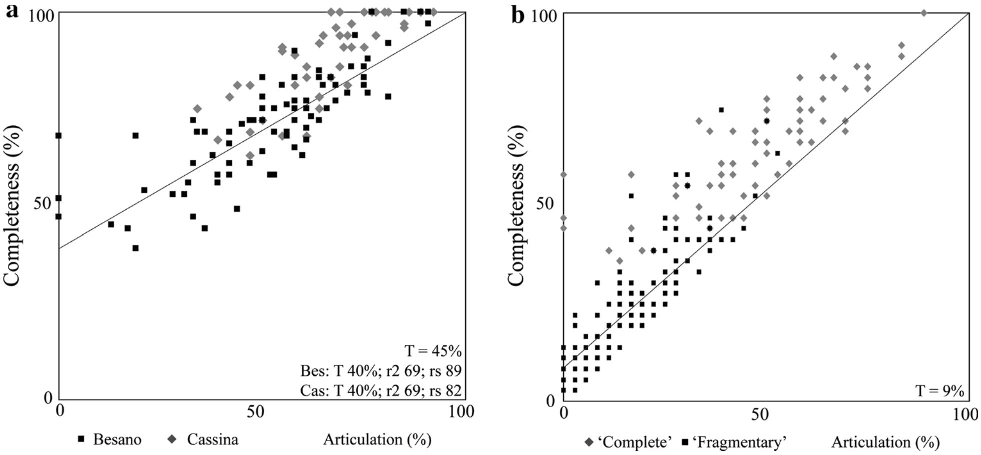


Fig. 3 Percentage data plotted as bivariate scatter plots. **a** Percentage data for 133 'complete' specimens of *Saurichthys* from the Besano Formation and Cassina Beds; **b** percentage data for the 362 *Saurichthys* showing 'complete' specimens as *grey diamonds* and 'fragmentary' specimens as *black squares*. Returned T, r^2 and rs values are shown for each plot where calculated

poorly articulated and incomplete. The T value calculated for these 133 *Saurichthys* is 45 %, a mid-Trend 3 distribution of data.

4.2 Preservation in each horizon

The percentage data for the Besano Formation (n = 83) covers most of the above described envelope with articulation ranging between 0–91 % and completeness 39–100 % (Fig. 3a). The data is distributed in the regions of near fully articulated and fully complete, and poorly articulated and incomplete with an absence of points in the region of low articulation and high completeness. This distribution is supported by a T value of 40 % (low Trend 3). The high r^2 (0.69) infers a good fit of the data to the linear regression line, and the high rs (0.89), a strong relationship between articulation and completeness.

Among the ten unit plots there is no consistently observed pattern of distribution although it is possible to divide the plots into three groups based on the T value and visual observation of points (Fig. 4). The first comprises only the head unit, which exhibits a distribution of data primarily in the region of variable articulation and high completeness but with some limited data indicating low articulation and variable completeness. The T value is relatively high (3.75) in comparison to the other units. The second group comprises the axial skeleton, scale row, caudal fin, dorsal fin and anal fin units, which share a wide distribution of data across most of the available field and moderate T values, when the possible maximum values of each unit is considered. It is noted that these plots also share a concentration of data at, or near, the maximum values of articulation and completeness. The final group is made up of the paired (pectoral and pelvic) fins, which exhibit a distribution of data described as Trend 2. This group could be further divided into the left and right pectoral fin units, sharing a concentration of data at minimum values of articulation and completeness (highlighting an absence of the unit in the majority), and the left and right pelvic fin units, showing a similar concentration of data along the diagonal between maximum to minimum values of articulation and completeness (Trend 2 in the strictest sense). The rs values for the unit plots, all above 0.5, suggest a moderate to good relationship between articulation and completeness. Although r^2 values are harder to divide in the same way, the left and right pelvic, and left pectoral fin units have the highest values (0.9, 0.89 and 0.94, respectively) suggesting a better fit to the linear regression line than the head and scale row units in particular (0.26 and 0.37, respectively).

The distribution of the percentage data for the Cassina Bed (n = 50) covers a relatively smaller field by comparison to the Besano Formation data (Fig. 3a). The data is distributed in the region of moderate to high articulation with values for articulation ranging between 34–91 %, and completeness 47–100 %. Despite this, the supporting values for the Cassina Beds (T 40 %; r^2 0.69; rs 0.82) are similar to those returned for the Besano Formation.

The ten unit plots for the Cassina Beds can be divided into four groups (Fig. 5). The first comprises the head and scale row units, in which data occurs only in the variable articulation and high completeness region and maximum T values are returned. Although the axial skeleton and caudal fin units also show a focus of data in the same region, they are separated from the head and scale row units to form a second group based on the presence of data representing other (lower) score combinations. The third group comprises the paired (pectoral and pelvic) fins, which exhibit strong Trend 2 distributions and low T values between 0.06 and 0.27. The final group comprises the unpaired dorsal and anal fins, which are more similar to each other than either is to any other unit. The plots can also be divided into two groups based on the rs values: the left and right pectoral, and left and right pelvic fins all have high values

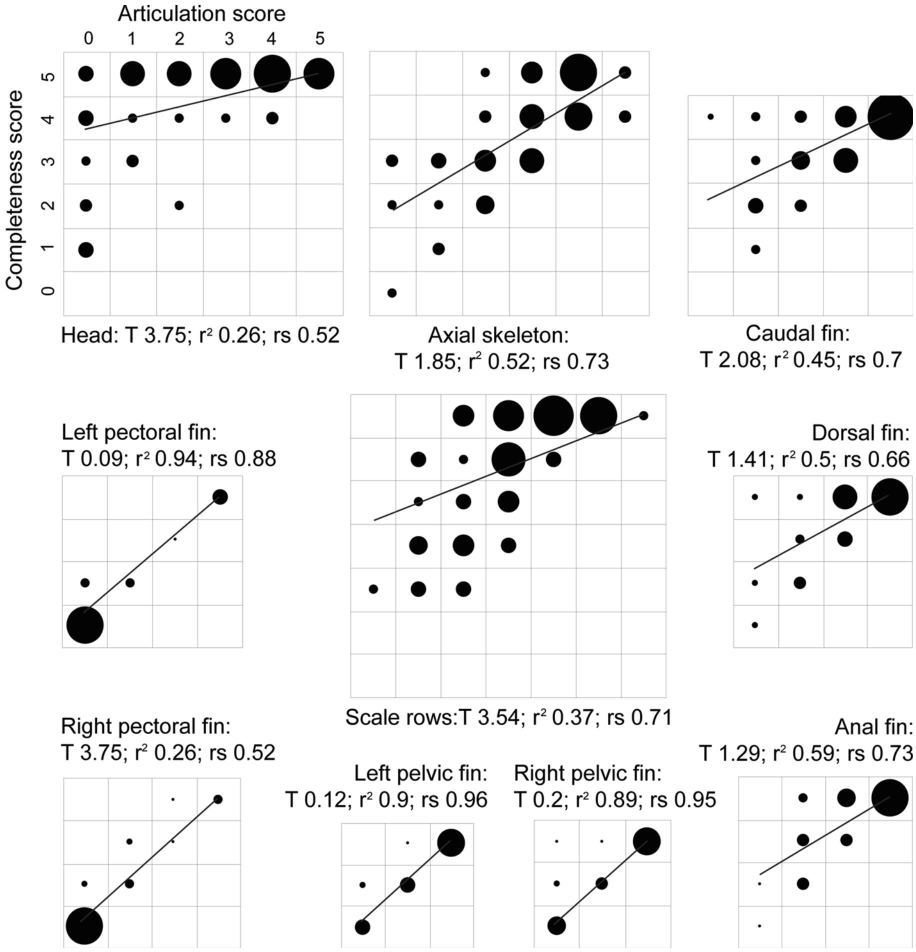


Fig. 4 Unit plots for *Saurichthys* from the Besano Formation. The designated units are the head, axial skeleton, caudal fin, left pectoral fin, right pectoral fin, scale rows, left pelvic fin, right pelvic fin, dorsal fin and anal fin as labelled. Returned T, r^2 and rs values are shown for each plot

above 0.9, suggesting excellent relationships between articulation and completeness, while the scale row, axial skeleton, caudal fin, dorsal fin and anal fin units have low to moderate values between 0.2 and 0.45; no value was returned for the head and scale row units. This division can also be made for the r^2 values, with the former group having high values above 0.8 and the latter between 0 and 0.45.

4.3 Size

Preservational variation relating to size was investigated by plotting total body lengths of *Saurichthys* separately against articulation and completeness (Fig. 6a, b). Specimens from each horizon cover a range of measurements from approximately 5–80 cm. In the Besano Formation, the majority are in the low to mid-range: between 5 and 50 cm. In the Cassina Beds the range is narrower and higher, between 20 and 50 cm. In terms of preservation, for specimens of a similar size, the plots indicate higher values of both articulation and completeness for *Saurichthys* in the Cassina Beds compared to the Besano Formation (Fig. 6).

4.4 Lithology

The *Saurichthys* from P. 902, 75 of the 83 Besano Formation specimens, are preserved in four main lithologies: black shale (20 specimens), and finely laminated- (7), laminated- (38) and massive dolomite (9) beds (see sections in Bernasconi 1991; Röhl et al. 2001). Values of articulation and completeness for specimens in laminated dolomite are distributed most widely, covering almost the entire envelope described above for MSG *Saurichthys* as a whole and the Besano Formation specimens (compare Figs. 3a, 7). Data for the other three lithologies is encompassed within this but only the finely laminated dolomite data has any focus in distribution, the data for this being found above 50 % articulation and 75 % completeness. Any further concentrations or patterns are not apparent (Fig. 7).

4.5 Variation at P. 902 (Besano Formation)

Articulation and completeness data for the 362 specimens was plotted as a percentage plot (Fig. 3b). Although this

Fig. 5 Unit plots for *Saurichthys* from the Cassina Beds. The designated units are the head, axial skeleton, caudal fin, left pectoral fin, right pectoral fin, scale rows, left pelvic fin, right pelvic fin, dorsal fin and anal fin as labelled. Returned T, r^2 and rs values are shown for each plot

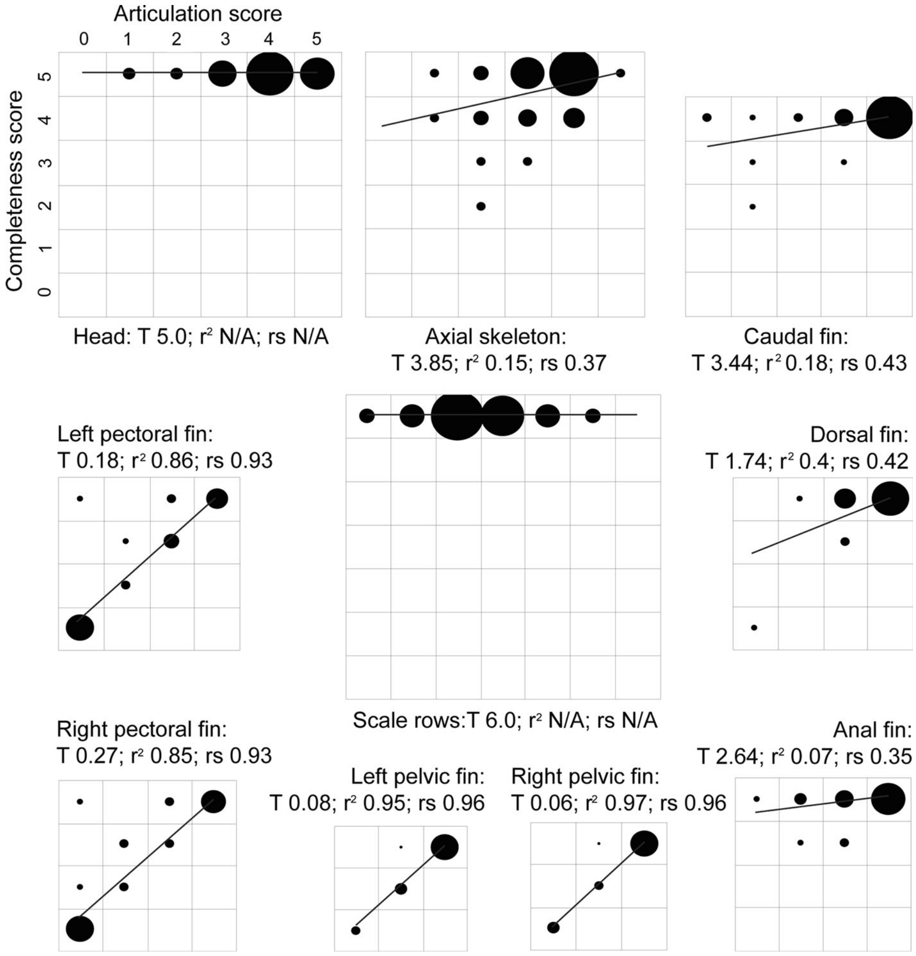
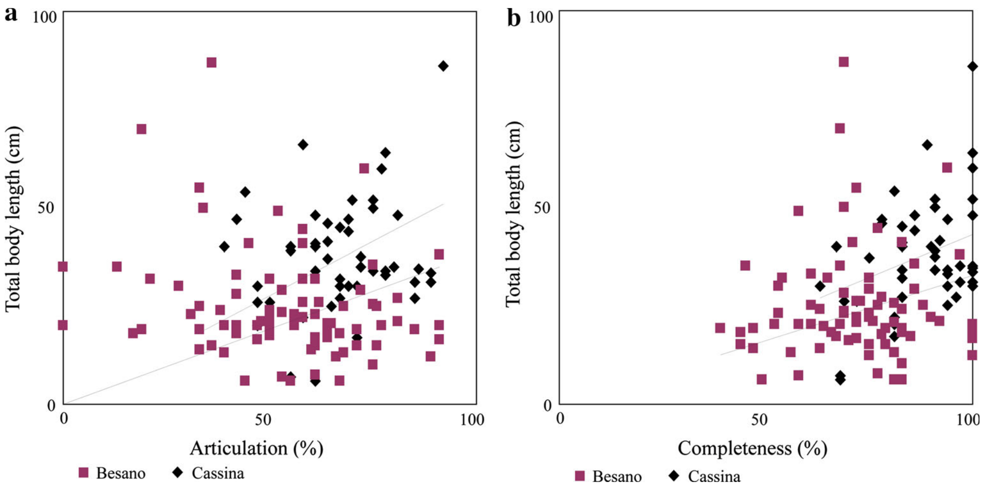


Fig. 6 Percentage data plotted against body length for specimens from the Besano Formation and Cassina Beds. **a** Data for articulation and **b** completeness. Measurements are given in centimetres



includes 83 specimens from the main analysis, there was no compensation in this second analysis for units marked with an X, therefore the position of some points differs slightly. The distribution of data more strongly follows a diagonal line from maximum to minimum values of articulation and completeness (compare Fig. 3a, b) with the majority of data focused in the region of low articulation and moderate to low completeness. Very few points indicate high articulation and high completeness, and data is entirely absent from the region of moderate to low articulation and high completeness. This distribution is supported by a calculated T value of 9 % (Trend 2).

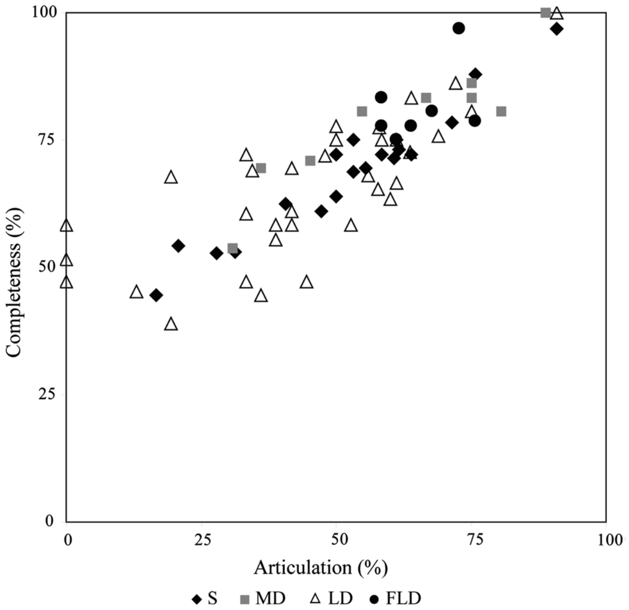


Fig. 7 Percentage articulation and completeness data for the four main lithologies in the Besano Formation at P. 902. *S* shale, *MD* massive dolomite, *LD* laminated dolomite, *FLD* finely laminated dolomite

The second part of this analysis investigated the preservation of specimens among beds in the Besano Formation at P. 902. Preservational values of articulation and completeness were plotted separately against bed number, of which there are 183 beds in the standard section at P. 902 (Rieber 1973; Röhl et al. 2001). Specimens in the dataset originate from 70 beds, with most sourcing no more than 12 (Fig. 8a). The exceptions are beds 148 (31 specimens), 152 (54, the highest for the section), 153 (25), 158 (14), 161 (18) and 164 (19). Data shows better articulation and completeness, and a broader range of values, in the upper compared to the lower part of the formation (Fig. 8b, c). Values for the fragmentary specimens show as much variation as the complete specimens, but the former occupies the lower half and the latter, the upper part, of the range for articulation and completeness for each bed.

4.6 Specific preservational features

During the scoring of units for *Saurichthys*, a number of repeated preservational features were observed:

4.6.1 Isolation of the head unit

Examination of the 362 *Saurichthys* in the P. 902 dataset found that many of the fragmentary specimens comprised of isolated head units but also a number of more complete specimens in which the head as a coherent unit was separated from, but still associated with, the remainder of the body (Figs. 9a, 10). Skulls in isolation were present in 59 of the beds that yielded specimens herein with no more than 12 in any one bed (Fig. 8d). It was also noted that in specimens showing only limited disarticulation of the head, the elements that separated were the opercles, the posterior elements of the skull and/or the lower jaw elements (Fig. 2).

4.6.2 Eye spots

Black circular or oval shaped spots within the orbital fenestrae of the skull were noted in specimens from 10 beds in the upper part of the Besano Formation with no more than 12 in any one bed (Figs. 8e, 9b). Most of these specimens were of small size and considered to be juvenile (36 of 41 exhibiting this feature). In contrast, the number of specimens from the Cassina Beds with the same feature was much lower (2 of 50) and these were of a larger, probably adult, size.

4.6.3 Fin units

Fins showing full, or near full, articulation as a unit can be separated from the remainder of the body by a distance of a few centimetres (Fig. 9c). The feature is most commonly seen in the unpaired dorsal and anal fins, but has also been observed less frequently in the paired pectoral and pelvic fins. The left and right of the pectoral fin units are more often entirely absent, which is unusual when all other units are at least moderately complete and/or articulated.

4.6.4 Twisting of carcasses

The orientation of a carcass relative to the sediment surface is commonly inconsistent along the length of the body. For example, the caudal fins normally lie in lateral orientation so that each lobe rests on the sediment surface but the head is not restricted to any particular angle given its overall barrel-shape morphology and the limited stabilisation provided by the pectoral fins, which can lie flat against the body. Interestingly, the body by the dorsal and anal fins tends to lie laterally so that these fins are flat against the sediment in the same way as the caudal fins but in a limited number of specimens the dorsal and anal fins appear to have folded over the body as if this region has been rolled. Such movement does not seem to affect the preservation of one or both fins, which are still at least moderately articulated and complete, highlighting the coherence of the soft tissue supporting the rays that comprise the fin units. In a few specimens the axial skeleton and the lateral scale rows can also corkscrew as if half of the body was rolled several times relative to the other in opposing directions (Fig. 9d). Again, these specimens do not show extensive disarticulation or loss of completeness.

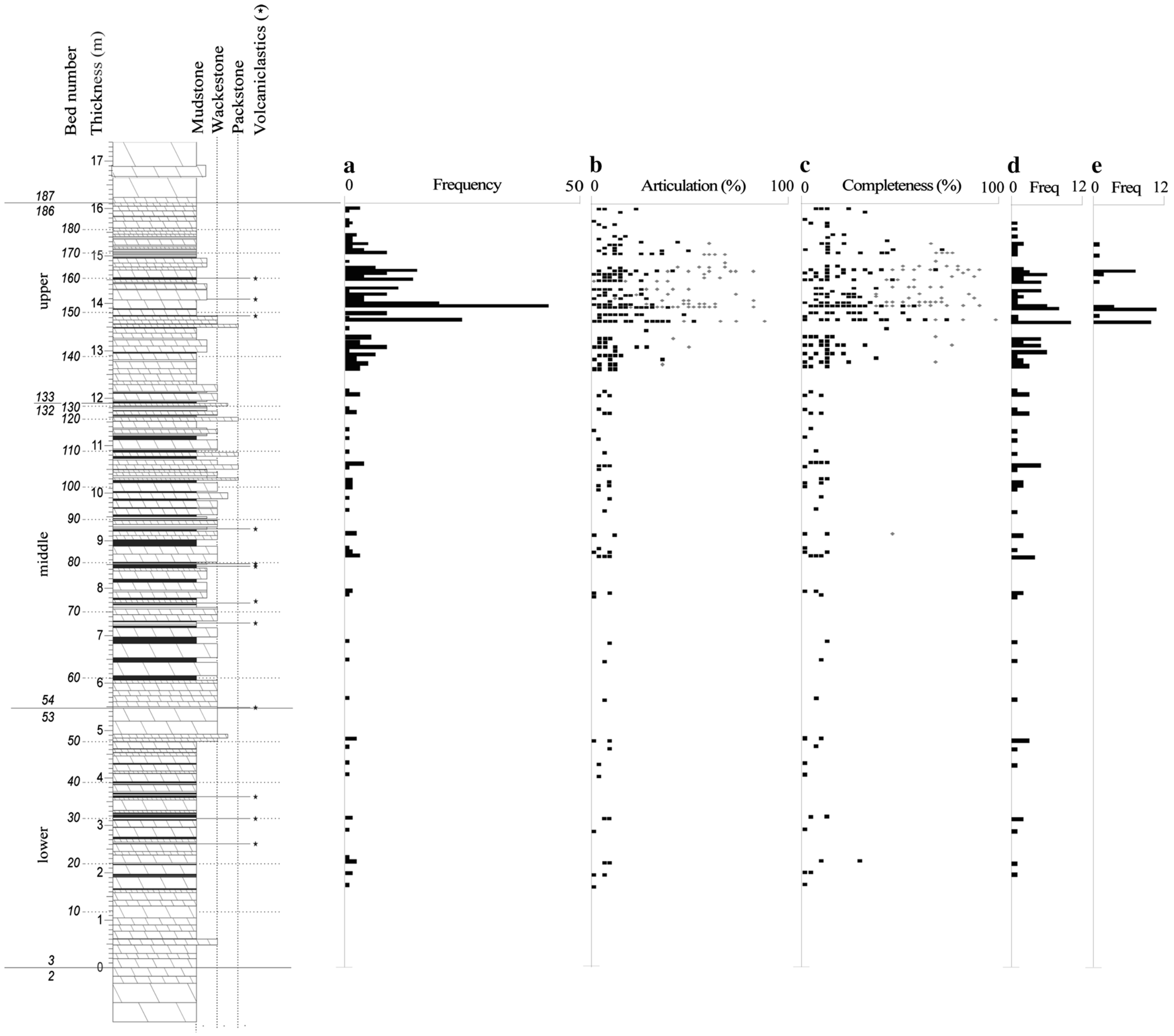


Fig. 8 Lithological section for the Besano Formation at P. 902 and distribution of several repeated preservational features. **a** The source level of the *Saurichthys* specimens used herein; **b** articulation values for specimens from each bed. *Grey diamonds* represent the complete specimens and the *black squares*, the fragmentary specimens; **c** completeness values for specimens from each bed. *Grey diamonds* represent the complete specimens and the *black squares*, the fragmentary specimens; **d** the occurrence of the head as an isolated unit; **e** the occurrence of black eye spots

4.6.5 *Localised disruption of abdominal elements*

The location of disarticulation in the axial skeleton tends to occur at particular points in the body, normally at the anterior-most end of the axial skeleton behind or close to the skull (Fig. 9a) and/or the mid-region of the body posterior to the dorsal and anal fins. Only elements in the near vicinity of these points are affected, being scattered randomly and without obvious alignment; those beyond are often still fully articulated. 'Ballooning' of the scale rows, bulging symmetrically out from the midline of the body, is also noted. Although a thorough investigation is still necessary there seems to be a greater number of specimens exhibiting these features in the Besano Formation (at least 25 were recorded) compared to the Cassina Beds (approximately 10).

4.6.6 *Features of the scale row and axial skeletal units*

Highly disarticulated axial skeletal units can show articulated chains of approximately 10–20 neural and haemal arches (Fig. 9c) (Maxwell et al. 2013). In fully articulated

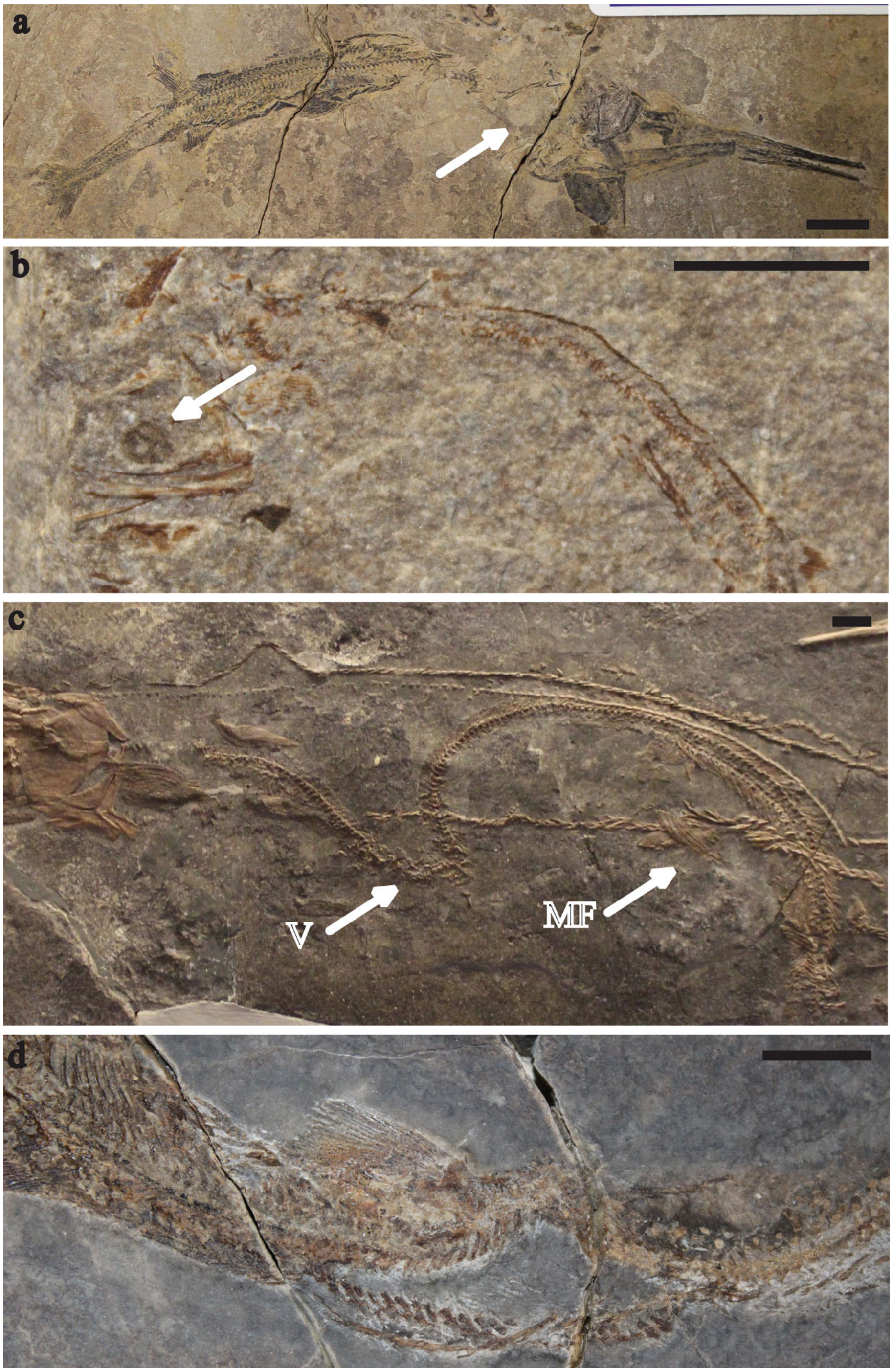


Fig. 9 Examples of repeated preservational features in *Saurichthys*. **a** Localised disruption in the anterior part of the vertebral column resulting in separation of the skull from the otherwise articulated and complete body (PIMUZ T 529 from the Besano Formation); **b** a black eye spot in a juvenile of *Saurichthys* from the Besano Formation (PIMUZ T 548 from the Besano Formation); **c** a specimen showing strong curvature of the axial skeleton to the extent it breaks out of the body outline provided by the mid-dorsal and mid-ventral scale rows (*arrow* marked V) and articulation of the mid fin units that are separated from the remainder of the body (*arrow* marked MF) (PIMUZ T 4154 from the Cassina Beds); **d** section of the abdominal region of a *Saurichthys* focusing on the scale rows and axial skeleton that both show twisting (PIMUZ T 668 from the Besano Formation)

Saurichthys, the scale rows tend to form bands that run the full length of the dorsal surface and three quarters of the lateral and ventral surfaces. These effectively form an outline of the body between which the axial skeleton runs. In some specimens, the axial skeleton shows such extensive curvature that either end of relatively long disarticulated segments 'break out' of the body outline formed by the scale rows but without disturbing it in any way (Fig. 9c).

5 Discussion

The taphonomic data for the main MSG *Saurichthys* dataset returned a moderate Trend 3 distribution and T value of 45 % (Fig. 3a; Beardmore 2012; Beardmore et al. 2012) inferring disarticulation of skeletal elements was accompanied by loss of completeness in many cases. The notable absence of the left and right pectoral fins supports this, however, evidence at several analytical levels suggests

Fig. 10 An example of a complete *Saurichthys* skeleton from the Besano Formation (PIMUZ T 1549) with all elements disarticulated except those of the head unit, which remains fully articulated. *Scale* as indicated

the loss of articulation and completeness was not simultaneous. At specimen level there is an occurrence of three data points representing entirely disarticulated *Saurichthys* (Fig. 3a), whose skeletal completeness has remained high enough for the scattered elements from each designated unit to be seen in the approximate regions occupied and relative to each other during life. At unit level, the head and several of the fins have been observed as fully or near fully articulated but separated from the remainder of the body. In short, skeletons tend to show some degree of articulation, which varies across the entire range of values, but completeness in most is maintained at or above a moderate level. This conclusion is supported by the findings of Renesto and Stockar (2009, p. 324) who suggested 'the presence of mostly complete and articulated fossils' in the Cassina Beds and described the three specimens of *Saurichthys* with embryos as mainly articulated and complete. Tintori (1992, p. 397) also described the vertebrates of the Besano Formation as 'wholly articulate' and suggested preservation of fish could be divided into those that were fully and only partially articulated.

The loss of articulation observed can potentially occur at any time during the death-burial interval, but, during transport and floating, it is automatically accompanied by loss of completeness. Simultaneous loss of articulation and completeness in *Saurichthys*, as stated above, does not occur in the majority of cases, suggesting arrival at the sediment–water interface was probably relatively soon after death. Alternatively, it has been considered that the high completeness might instead reflect the resistance of the integument to decay, which might prevent any elements that did become disarticulated from separating from the remainder of the carcass. However, a rapid transition to the sediment surface is more likely due to the heavy weight of the skull. Transition through the water column itself can also be inferred as steady, or with carcasses landing long axis parallel to the sediment surface, as penetration into substrate is known in only a few specimens and limited to the rostrum of the skull. Only after arrival at the sediment surface, during the residence phase of the death–burial interval, did the reduction of skeletal articulation and completeness observed in *Saurichthys* take place, as was also noticed for pachypleurosaurids (Beardmore 2012; Beardmore et al. 2012). In quiet bottom water conditions, the progression of disarticulation can occur passively as soft tissue decays, allowing elements to settle into a stable position by gravity. It can be inferred very generally that the greater the disarticulation of a skeleton the longer a carcass was exposed before final burial under sediment. The fact that *Saurichthys* show almost the entire range of articulation values suggests that the duration of the residence phase also varied considerably (Fig. 3a-b). Unusually, there is evidence of more active mechanisms of disarticulation in *Saurichthys* involving additional processes that initiated or exacerbated disarticulation. For example, the above described disruption to elements in the abdominal region could be caused through weakening of the tissues in the gut region as decay progressed, resulting in deformation of the scale rows by gravitational collapse however the localised disarticulation and scattering of elements in the immediate area cannot be explained by gravity alone. Current activity has been inferred at various beds at MSG but would affect the whole carcass rather than focused regions (Sander 1989; see also below). The disruption could be the effect of initial bloating by accumulation of decay gas in the pectoral area just after death in the warm surficial water, as noted by Schäfer (1972), Stockar (2010) and discussed by Maisey (1991). However, as the deposition of the integral carcass occurred in deeper water (30–130 m water deep), further bloating was not possible due to high hydrostatic pressure and probably cold and anoxic bottom water (see Reisdorf et al. 2012, 2014).

A further explanation for the disruption to the abdomen, and other anatomical regions, could be the apparent fixing of parts of the carcass to substrate, specifically the scale rows that effectively form an outline of the body, and the mismatching axial skeleton that breaks through it in several specimens (Fig. 9). The method of fixing was potentially microbial mats growing at the sediment–water interface or substances seeping from the decaying carcass (Bickart 1984; Briggs 1995; Furrer 1999; Renesto and Stockar 2009; Stockar 2010; Stockar et al. 2013; Orr et al. in review); both of these processes cannot immediately adhere a carcass to substrate but take days or weeks to form to the extent that body parts would remain fixed in place (Bickart 1984; Stockar 2010). The fact that the feature is evident in *Saurichthys* in the first place is due to the position of the axial skeleton in many specimens. That is, the normally relatively straight axial skeleton shows extensive curvature, suggesting it was subject to a process affecting the entire length of the body, but focused in the axial skeleton and probably the soft tissue surrounding these elements, and that was in effect over a sustained period of time (Fig. 9). The force exerted was in the end sufficient to snap the axial skeleton into several sections that each show curvature. Strong, but continuous, curvature has been observed in other vertebrates from MSG, notably the protorosaurs *Tanystropheus* and *Macrocnemus*, in which the long neck and sometimes tail curl back to meet the trunk region (Peyer 1937; Wild 1974; Beardmore 2012). Although the cause is still subject to discussion (see Reisdorf and Wuttke 2012), and beyond the scope of this study, in the case of the MSG *Saurichthys* acquisition of curvature in the axial skeleton can be concluded as post mortem. A carcass had to become fixed to the sediment and a sufficient shortening force exerted on the axial skeleton to cause it to bend and eventually break. All of the above preservational features were observed in several specimens from both the Besano Formation and Cassina Beds, suggesting that the residence phase at the sediment surface was crucially a minimum of several days, but was more likely to be on the week or even month timescale.

Despite the above described commonalities, there are enough differences in the results of the semi-quantitative analyses to suggest there is preservational variation between specimens from each horizon. At the highest percentage level, the strong overlap of data suggests that the same states of moderate to high articulation and high completeness occur in specimens from both horizons, but states of low articulation and moderate completeness are only present in the Besano Formation *Saurichthys* (Fig. 3a). The extension of the preservational field by the Besano Formation specimens, beyond that of the Cassina Beds, is also observed between corresponding unit plots, most obviously, in the head and scale row units (compare Figs. 3, 4). T values for units are also consistently lower for the Besano Formation. Together, these features imply not only a greater range in the loss of articulation and completeness but also that loss was able to progress much further in *Saurichthys* from the Besano Formation to result in specimens with low, or no, articulation and moderate completeness. The strong Trend 2 (T = 9 %) distribution for the dataset of 362 *Saurichthys* (Fig. 3b) suggests reduction of articulation and completeness could progress further still, to the stage where units, notably the head, became disarticulated from the remainder of the body and, subsequently, were isolated. In short, the datasets used herein and the results they returned seem to represent steps in a single taphonomic path from mostly articulated and complete skeletons (Cassina Beds), to poorly articulated and moderately complete skeletons (the more ‘complete’ Besano Formation specimens), and eventually disarticulated skeletons or isolated units (‘fragmentary’ specimens from the Besano Formation). Whether the latter step is also evident in specimens from the Cassina Beds was beyond the scope of this study but is potentially testable in the future as fragmentary specimens from the horizon are also available in the PIMUZ collection.

What facilitated the reduction of articulation and completeness through the steps of the taphonomic pathway is almost certainly the surrounding environmental conditions. Both horizons were deposited in the same subsiding, intraplatform basin (the Monte San Giorgio Basin), under a stratified water column, restricted in the most part from more open marine conditions, and with influxes of allochthonous sediments and organisms from surrounding carbonate platforms during monsoonal storms (Rieber 1973; Sander 1989; Bernasconi 1991; Furrer 1995, 2003; Röhl et al. 2001; Stockar 2010; Beardmore 2012; Beardmore et al. 2012; Stockar et al. 2013). Conditions with enough strength and intensity to exacerbate disarticulation and cause loss of completeness, and that could have varied between the Besano Formation and Cassina Beds, are therefore limited. One difference is water depth, estimated to have been well below maximal storm base (30–130 m) for the Besano Formation and just below maximal storm wave base (30–40 m) for the lower Meride Formation (Bernasconi 1991; Furrer 1995; Röhl et al. 2001; Stockar et al. 2013). Another difference is the sedimentation rate, which is much lower in the Besano Formation than for the Cassina Beds, the latter comprising more numerous and thicker beds of allochthonous carbonate mud and sand. Based on old chronostratigraphic data, the compacted sedimentation rate for the Besano Formation was estimated to 5 mm/kyr (Bernasconi 1994; Furrer 1995) however, newer radiometric dating of volcanic ash layers in the middle Besano Formation (242.1 ± 0.6 Myr, Mundil et al. 1996, 2010) and in the Cassina Beds (240.63 ± 0.13 Ma;

Stockar et al. 2012) give a compacted sedimentation rate of about 15 mm/kyr for the Besano Formation, and 32 mm/kyr for the laminite facies of the Cassina Beds (Stockar et al. 2012).

A commonality in previous taphonomic studies, specifically of MSG reptiles, is the suggestion of weak bottom currents. Sander (1989) inferred this feature, based on the alignment of individual bones and skeletal postures in the pachypleurosaurids *Neusticosaurus* and *Serpianosaurus*. Beardmore (2012) went on to propose a taphonomic model for these taxa, in which the slower rate of sedimentation in the Besano Formation led to a prolonged residence on the sediment surface in *Serpianosaurus* when current activity impacted on the completeness of the carcasses. By comparison, residence was shorter for *Neusticosaurus* resulting in their better articulation and, especially, completeness. The taphonomic model for the protorosaur *Tanystropheus* also involved a combination of three main factors: sedimentation rate, current activity and size (Beardmore 2012). The latter was highly variable, from 50 to 450 cm, and when correlated with preservation revealed a complicated 'goldilocks' relationship whereby the largest specimens were better preserved due to the decreased effect of current activity on their larger and heavier elements, as were the smaller specimens that were more rapidly buried by sediment due to the smaller size of elements comprising their skeletons, compared to moderately sized specimens between that suffered the effects of current activity during prolonged residence on the sediment surface. For *Saurichthys*, a combination of factors, specifically sedimentation rate, residence duration and current activity, is also indicated. That is, the higher rate of sedimentation would have allowed more rapid burial of *Saurichthys* preserved in the Cassina Beds compared to those in the Besano Formation. The variable but generally prolonged residence on the sediment surface, especially for the Besano Formation *Saurichthys*, is supported by several preservational features, notably the greater progression of disarticulation with only a moderate loss of elements. Direct evidence of current activity, such as alignment of skeletal elements is not apparent, even where elements have been disarticulated and scattered; parallel orientation of body parts, such as that described for the neck and tail in *Serpianosaurus* (Beardmore et al. 2012), was not attainable due to the overall less flexible morphology of *Saurichthys*. There was also no greater loss of articulation or completeness from smaller *Saurichthys* skeletons compared to those of larger size (Fig. 6). If currents were present in either the Besano Formation or Cassina Bed setting they were not particularly intense or consistent, but are considered the most probable cause for the limited loss of completeness and the rolling and twisting observed in carcasses.

A final point is the consideration that some of the patterns in preservation are artefacts of excavation. The results of the bed-by-bed investigation of preservation indicated articulation and completeness were higher, and that the scatter of values increased to cover almost the entire range of each, in the upper part of the Besano Formation. The patterns initially support the suggestion of variation on this scale, however the greater surface area of strata excavated at P. 902 in the upper part (240 m^2 relative to 90 m^2 in the lower part) could potentially have resulted in recovery of a higher number of specimens. Why complete specimens are more common in the upper part of the formation is still unclear. A study of sedimentology and microfacies does however document that the upper part of the Besano Formation is dominated by finer carbonate (mudstone), whereas the middle part is characterised by coarser carbonates (wackestone and packstone) intercalated with muddy black shales (Röhl et al. 2001). The black shale is proposed to have a low sedimentation rate interrupted by rare events with deposition of coarser material (detached turbidites, Bernasconi 1994) while the rate for the dolomitic mudstone of the upper Besano Formation was much higher. These features should be investigated further as a possible explanation of preservational differences.

6 Conclusions

The investigations of taphonomy in *Saurichthys* from Monte San Giorgio indicate the following:

- The taphonomic model for *Saurichthys* began with death at some level within the stratified water column of the Monte San Giorgio Basin, followed by minimal floating in the water column and a rapid transition to the sediment–water interface. Reduction in the condition of carcasses occurred during the residence phase on the seabed.
- The *Saurichthys* lay on the sediment surface for variable and often prolonged lengths of time. This is attested to by adhesion of carcasses to the sediment surface, the curvature of the axial skeleton sufficient to break it, and the damage to the abdominal region, which are all features that take several days or weeks to develop.
- Disarticulation occurred as decay progressed but loss of completeness was the result of environmental features. The end result for *Saurichthys* was either a fully disarticulated skeleton or the isolation of parts of the carcass, notably the head unit, from the remainder of the body.
- Preservational differences exist between specimens from the Besano Formation and Cassina Beds of the

Meride Formation that can be attributed to differences in the depositional settings for each horizon. That is, specimens in the Besano Formation underwent a longer residence on the sediment surface, due to a slower sedimentation rate, and in turn were exposed to weak bottom currents for longer, resulting in the greater variability and progression in the loss of articulation and completeness. Weak bottom currents were probably also responsible for the rolling of carcasses and potentially exacerbated disarticulation in the long term.

- Future work should focus on the investigation of small scale, bed-level preservational variation in the Besano Formation at P. 902 to identify more conclusively the extent of variation and in turn any causal features. There is the potential for a similar study to be undertaken for specimens from the Cassina Beds at the same scale.
- The study importantly highlights how using more 'complete' specimens alone presents only half of the taphonomic story and that the information from 'fragmentary' material should also be sought.

Acknowledgments We would like to thank T. Brühwiler, C. Egli, J. Huber, H. Lanz, L. Pauli (all PIMUZ), C. Obrist (Rickenbach BL) and U. Oberli (St. Gallen) for their excellent preparation of the specimens. B. Jost (PIMUZ) drew Fig. 1. We also appreciate useful comments by two anonymous reviewers. This project was funded through the Swiss National Science Foundation (SNF) Sinergia Grant CRSII3-136293 to M. Sánchez-Villagra, H. Furrer, and W. Salzburger.

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